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STUDIES IN ROOT-PARASITISM.

THE HAUSTORIUM OF OLAX SCANDENS.

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THE HAUSTORIUM OF OLAX SCANDENS.

In previous papers of this series the Haustorium of *Santalum album* was described in considerable detail.[1] It was at the same time noted that certain *Olacaceæ* had been found to be green root-parasites in much the same manner as the sandal. Collections have been made in South India of haustoria of *Cansjera Rheedii*, *Olax scandens*, *Ximenia americana* and *Opilia amentacea*. The present paper deals with the parasitism of *Olax scandens*, this plant having been selected because of important differences between its haustorium and that of *Santalum album*. These differences are less marked in the mature haustorium, and lie chiefly in the manner of development of the various tissues, the limits of nucleus and cortex, the formation and structure of the gland, the number of cortical folds, the composition and place of origin of the collapsed layers and the arrangement of the vascular system. In most of these characters the haustorium of *Olax scandens* appears to differ from those of the other haustoria named above as well as from those of *Osyris* and *Thesium* and, in describing it, these characters will be dealt with much more fully than those in which there is agreement with the haustorium of *Santalum album*.

A careful perusal of the literature on root-parasites reveals the fact that suggestions have been offered in the past as to the

[1] Studies in Root-parasitism.—The Haustorium of *Santalum album*. Part I.—Early stages, up to Penetration. Part II.—The mature Haustorium. Memoirs Dept. Agri. India, Botanical Series, Vol. I, No. 1, Parts I and II—1906-07.

parasitic nature of the *Olacaceæ*, but, just as similar suggestions regarding *Santalaceæ* were long before they bore fruit, those on the *Olacaceæ* have been disregarded. So important a character as parasitism could not have been without interest to systematists, and the absence of all knowledge on the subject must be put down to the fact that the bulk of the systematic study of the higher plants is carried on in herbaria, where large collections of dried branches are stored, and therefore far away from the natural haunts of the plants themselves.

The parasitism of *Thesium humifusum* was proved by Mitten[1] in 1847 : Planchon[2] discovered that of *Osyris alba* in 1858 : Scott[3] noted the parasitism of *Santalum album* in 1871 : comparatively recently Shirai[4] discovered that *Buckleya Quadriala* possesses the like character. And in most of these cases, if not in all, the discovery was made quite independently of the known occurrence of this character in the Order. Planchon, when he found haustoria on *Osyris*, remarked that probably all *Santalaceæ* and, from their affinity, *Olacaceæ* would prove to be root-parasites, but neither this nor Heckel's note[5] on the parasitism of *Ximenia americana* seedlings produced any further results. The discovery of root-parasites among *Olacaceæ* in South India was, as already described (*Santalum*, Part I), made quite accidentally while searching for haustoria of *Santalum album*.

2. *Olax scandens* is a sprawling shrub growing in the midst of thickets. Its trunk is not usually very conspicuous, but sometimes reaches 6—8 inches in thickness, with numerous dorsiventral,

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[1] W. Mitten, Sur le Parasitisme des Racines du *Thesium humifusum*. Ann. d. Sc. Nat. III Ser. Bot. 1847. Vol. 7, pp. 127-8.

[2] J. E. Planchon, Sur le Parasitisme de l' *Osyris alba* (C. R. d. l' Acad. d. Sc. 26 July 1853). Bull. d. l. Soc. Bot. d. France, V., 1858.

[3] J. Scott, Loranthaceæ . . . germination and mode of attachment. Journ. Agri-Hort. Soc. Ind. II, 2, 1871.

[4] S. Kusano, Studies on the Parasitism of *Buckleya Quadriala*, B. et. H., a Santalaceous Parasite, and on the structure of its Haustorium. Journ. Coll. Sc. Imp. Univ., Tokyo, Japan, xvii, 10, 1902.

[5] A. Heckel, Sur le Processus germinatif dans le graine de *Ximenia americana L.*, et sur la Nature des Ecailles Radiciformes, Rev. gen. d. Bot. XI. 401-9. 1899.

half-climbing branches. It is thorny, but only on the older parts of the stem. The leaves are two-ranked, oval or oblong, shortly petioled, dark green, with a blunted apex, 2—3 inches long and 1 inch broad. In the axils of the leaves there are small bunches of whitish, sweet-scented flowers and, later on, globular or ovate fruits. The latter are whitish in colour and have yellow flesh.

The plant occurs all along the eastern coast of the Madras Presidency and for a considerable distance inland, chiefly at low elevations. It is also found in the low, dry part of Ceylon and various parts of Northern India. It is common in Burma and is found in Java. It belongs to a small genus of 25—30 species confined to the tropical parts of the Old World.

Its associates in South India are pretty generally indicated by the appended list of the hosts examined, all ordinary inhabitants of the mixed (evergreen and deciduous) plains' flora of the east coast. This flora is adapted to withstand great heat and drought but in places receives from 30 to 40 inches of rain during the wet half of the year. Leguminous trees such as *Acacia arabica*, *A. leucoxylon*, *Dichrostachys cinerea*, *Pithecolobium dulce*, *Pongamia glabra*, *Albizzia Lebbek*, *Cassia siamea*; *Azima tetracantha*, *Capparis* sp., *Streblus asper*, *Morinda tinctoria*, *Melia Azidarachta*, *Feronia Elephantum*: climbers like *Jasminum sessiliflorum*, *Tragia involucrata*, *Rivea hypocrateriformis*, *Asparagus racemosus*, *Solanum trilobatum*: succulents such as *Opuntia Dillenii*, *Jatropha gossypifolia*, *Vitis quadrangularis*; and various small shrubs and herbs found in waste places or under the shade of trees, *Ruellia*, *Phyllanthus*, *Phaseolus*, *Ocimum*, *Carissa* and the smaller *Cassias*. All of which are dwellers on the Coromandel coast.

3. The fruit is a drupe of somewhat curious form, apparently arillate from the fusion of the accrescent calyx with the pericarp to near the top (Plate I, fig. 1). The single seed is heavy and filled with oily endosperm in which lies the minute cylindrical embryo. The radicle is superior. The abundant food in the seed enables the young plant to lead an independent life for a

considerable period. The fruit is said to be relished by birds, and would thus be carried from one tree to another and there dropped among the roots. We find a similar arrangement in the fruits and seeds of *Santalum*, *Cansjera*, *Buckleya*, and *Osyris*, while the smaller fruit of *Thesium*, surrounded by its fleshy calyx, falls at the base of the plant among the grass roots. Such thick-sowing ensures the presence near at hand of the roots of other plants and also explains the half-gregarious mode of occurrence so often seen in root-parasites. So in the *Rhinanthaceæ* we hear of comparatively heavy seeds and germination of the young plants at the foot of their parents' stems, forming the "milky ways" of the Eyebright and causing the Yellow Rattle to be found in such masses as to suggest their having been "sown by the bushel." [1]

Upon germination the root emerges, carrying with it a warty mass of endosperm reminding of a carbuncle, becomes positively geotropic and passes downwards. The cotyledons increase in size and form two plates folded on one another in the endosperm (Plate I, fig. 4), their free surfaces developing a well-marked epithelial absorbent layer. A great extension of the hypocotyl now takes place and, as in *Santalum*, forms a green loop above ground connecting the root and seed. The cotyledons are soon broken off at the base and are left behind in the empty seed, while the young stem is borne aloft and the first pair of leaves unfolded. These stages are illustrated in figures 2—5 on Plate I.

4. As it was not found possible to observe the seedlings of *Olax* in nature, a number of seeds were sown in pure sand in pots in a garden in Madras. In 40 days the young plants had attained a length over all of about six inches, a pair of small green leaves being unfolded two or three inches above the surface. Below ground a sinuous tap-root gave off secondary horizontal branches at intervals. The whole root-system at this stage as

[1] Kerner and Oliver, Natural History of Plants, I, 184. 1894.

well as part of the hypocotyl below ground was covered with a thick coating of root-hairs. In place of the radish-like swelling of the sandal seedling, the lower part of the stem and the upper part of the tap-root were more or less thickened, doubtless acting, as in sandal, as a store-house for reserve materials to the young plant.

The series of seedlings in these pots were examined at intervals for some 16½ months, when the experiment had to be discontinued. The root-system developed rapidly under these conditions, as in the similar experiments with *Santalum*, forming a dense mass of copiously branching rootlets. This root-system attained its maximum in about the sixth month and, by this time, some half dozen leaves of small size had appeared (Plate I, fig. 6). But these leaves lacked the bright green colour of the first pair: as time went on they became chlorotic and many of them dropped—evident signs of lack of nutrition. Comparatively few haustoria were at any time found in the pots but, at any rate while the roots were healthy, there was a fairly copious supply of root-hairs. These disappeared entirely in the later stages, a number of swellings appearing at the same time which were traced to an attack of eelworms (*Heterodera radicicola*).

At one year, the plants were all of them in a struggling condition, the leaves yellow and dropping and the root-system devoid of the finer branches and, as in sandal, covered with dark scars (Plate I, fig. 7). Some of the young plants were then transferred to ordinary garden earth, and these during the next few months showed much improvement, new roots being formed and the leaves assuming again the dark green colour of the earlier stages.

From these incomplete observations it would appear that *Olax scandens*, like *Santalum album* and many other parasites, develops at first like an ordinary non-parasitic plant, that it is capable of living for a long period upon the nutriment stored in its endosperm and, later, in its swollen stem and tap-root. Its rich development of root-hairs speaks of nutriment derived from the soil, and the brightening of the year-old plants when transferred from pure sand to vegetable mould suggests a considerable independence of growth. It is unfortunate that experiments

were not tried in growing seedlings in garden earth from the commencement, but those grown in sand were chiefly intended to supply material for the study of the young stages of the haustorium, in which respect the results were disappointing.

The difference from *Santalum album* in the development of root-hairs is not confined to the young plants, for in old roots in nature the parts immediately behind the broad white ends were found to be covered with a felt-work of delicate hairs, in striking contrast to the smooth white rootlets in sandal (Plate II, fig. 3). On the other hand, the copious development of haustoria on the young roots grown in sand, so striking a character in *Santalum*, was much less evident in *Olax*. A few haustoria were found, but they were widely scattered, few self-attachments were met with and not nearly so many cases of adhesion to pebbles or grains of sand (Plate II, fig. 4).

The free development of unattached haustoria in *Santalum* was regarded by Scott as indicating waning parasitism. This character must be extended to *Thesium* where many haustoria are unattached in the young roots, as has been pointed out by Leclerc du Sablon and others and observed by myself in Indian species. In both of these genera the root-system, as such, is poorly developed and root-hairs are more or less absent. These facts appear to indicate not so much a waning parasitism as a very well-developed one. In *Olax* on the other hand, the comparative rarity of haustoria in the earlier stages of growth, the well-developed root-system and the abundant root-hairs even in old plants, suggest rather *incipient* parasitism. According to Heinricher,[1] in plants becoming parasitic, haustoria are probably first developed, and then reduction of the root-system takes place. The parasitism of *Olax scandens* thus appears to be in a comparatively elementary stage, judging by the absence of the multitudes of unattached haustoria in the seedlings, the well-developed root-system and the abundance of root-hairs in both

[1] E Heinricher, Die grünen Halb-Schmarotzer, II *Euphrasia*, *Alectorolophus* and *Odontites*. Jahrb f. wiss. Bot. XXXII, 1898.

young and old stages of the plants. For the illustration of these points the reader is referred to the figures on Plates I and II.

5. The haustoria of *Olax scandens* differ but little in appearance from those of *Santalum album*. More or less conical, whitish as a rule, but frequently discoloured grey or brown by the surrounding earth or, in older specimens, by the corky layers formed and, in the latter case, lacking the bright red-brown colour of the sandal root-system. The older haustoria are perhaps more irregular than those of sandal and appear, on the whole, more frequently to be compressed and distorted or flattened, scale-like and circular. In size there is little to separate the two, the ordinary haustoria in *Olax* being 1—5 mm. high, 5—10 mm. long and 4—8 mm. broad (Plate II, figs. 5—8 of which 6 and 7 are of natural size).

Occurring as it does in thickets, *Olax scandens* has abundant roots at hand to which to attach itself, and examination shows that it avails itself very readily of the opportunity. It was also noticed at the very commencement with what frequency self-attachment occurred in nature. Indeed, the very first specimen which drew attention to its parasitism was the case drawn in figure 8 of Plate I, where a seedling has attached itself by a series of haustoria to another, older *Olax* plant.

Nothing definite can be said regarding the preferences of *Olax* roots for particular hosts. The only means available of judging was to determine in how far it was easy to collect haustoria from the plants growing near or with it, a matter depending largely on opportunity and locality. In the area from which the specimens were obtained, the following have earned the character of being favourites :—*Albizzia Lebbek*, *Casuarina equisetifolia*, *Jatropha gossypifolia*, *Pithecolobium dulce*, *Pentatropis microphylla*, *Dichrostachys cinerea*, *Azima tetracantha*, *Cephalandra indica* and *Feronia Elephantum*. On the other hand certain plants, occurring in fair abundance among the *Olax* thickets, were searched repeatedly with little success for connections. Such were *Euphorbia reticulata*, *Cassia siamea*, *Melia Azidarachta*,

Zizyphus Jujuba and Opuntia Dillenii. It is not, however, possible to form any definite conclusions on this point without a very great deal of study in other localities. All that can be said is that, from the very limited series of plants in which the roots have been laid bare, there are some grounds for assuming a certain amount of preference for certain hosts.

6. In the many haustoria examined in the preparation of this paper, a number of young ones, attached but not yet penetrated, were encountered, and a study of these has proved to be of exceptional interest (Plates III—VI). No attempt will be made here to trace the embryonic stages of the haustorial development or to determine the tissues of the mother root from which they were derived. It will suffice to say that there are evidences that the development of the haustorium from the mother root is similar to that described by Leclerc du Sablon[1] for *Thesium* and assumed by me for *Santalum*, but it will serve a better purpose to deal with this subject in several species together and the necessary material has not as yet been collected.

In its first appearance the haustorium of *Olax scandens* resembles that of *Santalum album* closely. The root-system of the pot-plants which were expected to furnish many young stages proved disappointing, but a certain amount of material was collected in nature (Plate II, fig. 2). It may be noted that even in the youngest stages the haustoria were smooth, although the roots on which they occurred were well clothed with root-hairs. This appears to be rather unusual among root-parasites. Root-hairs have frequently been noticed on the haustoria of *Santalum*, while they appear to be a constant feature in the *Rhinanthaceæ*.

The haustoria in *Olax* appear to be able, as in sandal, to develop without the aid of foreign root-stimulus, but proofs of this are not so clear as in that plant. Be that as it may, many of the haustoria become fairly large before they

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1 Leclerc du Sablon, Recherches sur les Organes d'Absorption des Plantes Parasites (*Rhinanthaceæ et Santalaceæ*). Ann. d Sc. Nat., Bot., Ser. VII, vol. vi, pp. 90-117, 1887.

make any impression on the root attacked. We shall proceed to consider the internal structure of such.

In the earliest stages of development met with in the sections examined a differentiation has already occurred in the tissues. These are divided into an outer and an inner zone (Plate III, fig. 1). A peripheral zone of irregularly arranged, more or less permanent cells surrounds the whole of the rest as a sort of mantle. The contents of these cells have largely disappeared, there is little or no starch, and rows of calcium oxalate crystals have made their appearance. Not infrequently the cells are crushed in places and intercellular spaces occur here and there. This crushing of the tissues is most pronounced at the inner border of the zone where it joins the central mass, and here too the intercellular spaces are not infrequently united to form a series of lacunæ.

The inner zone is at once seen to be the living, active part of the haustorium. The cells are small and full of contents, arranged in radial rows and rapidly dividing in a plane parallel to the surface of the host. Curves of growth are thus produced. In the case figured they are already commencing to bend inwards towards the middle line.

At the proximal end the vascular elements of the mother root enter the haustorium, bringing the materials for its development (Plate III, fig. 2). Where, as in fig. 1, the section is not quite median, masses of smaller, darker cells indicate the place where the vascular loop will make its appearance and unite the haustorial axis with that of the mother root. These procambial masses are formed in the zone of radiating cells.

There is yet another differentiation which has already made its appearance. The contents of the radiating cell are not equally distributed through the zone. The parts nearer the host's root are distinctly clearer than those outside them and, in thick sections, a band of cells with darker, starchy contents may be traced right round near the line of separation of inner and outer zones. This dark area forms a sort of cap over the inner, clearer portion and it is presumed that it is due mainly to the greater

meristematic activity in the distal end of the haustorium. There is less opportunity for the deposition of starch where the cells are in such active division, and the deposition of such starch indicates a tendency in the cells to cease dividing and become permanent.

7. Shortly after the haustorium comes into contact with the root of a host, important changes take place in its tissues. An oval area of clear cells altogether free from starch appears among the radiating cells in the median line. This oval area is the first indication of the "nucleus" of the haustorium, the parts on either side forming the "cortex" (Plate III, fig. 2). It should be borne in mind that these terms are purely empirical and a matter of convenience. The regions so called do not correspond with definite portions of the mother root, nor are they homologous altogether with the similar regions in the haustorium of *Santalum*. The term "nucleus" in any haustorium refers to that median portion which in early stages is differentiated by the character of its cell contents from the parts outside, undergoes rapid cell division and takes the chief part in the formation of the axis. It is probably only the lower part of the oval area now described which forms the nucleus in *Olax*.

The cortex of the haustorium is seen to consist partly of the outer permanent mantle of irregularly arranged cells already mentioned and partly of that portion of the radiating rows of cells of the last stage which are not included in the nucleus, but clothe it on either side. While thus the nucleus is employed in cell division and its cells are prevented from growing in length by the opposition of the host's root, the cortical cells expand and grow along the outer side of the root attacked, forming the cortical or clasping folds which thus early help to fix the haustorium to the host. This takes place with a certain amount of force, as is evidenced by the burrowing action of the folds in the bark of the host (Plate III, fig. 2).

The outer, irregularly arranged cells have become a permanent mantle round the tissues inside them, perforated at the proximal end by the strand of vessels from the mother root.

The denser portion of the cortex, laden with masses of starch, now occupies a position half way between the surface of the haustorium and the host's root. It has become more sharply defined and, in most cases, the outer radiating cells, formerly filled with starch, have commenced in their turn to lose their contents. The denser portion is moving inwards. A separation layer will shortly be found between the outer, denser part of the cortex and the inner, clearer rows of cells. Although this line of demarcation is not yet clearly seen, it is frequently possible at this stage to form an idea as to where it will be formed.

The haustorium, as a whole, is becoming crescent-shaped, and the lines of growth curve more distinctly towards the median line. This is brought about by the expansion of the outer cells of the radial rows tangentially, and they are seen to be distinctly broader than those within (b and c). The inner, clearer cells are in fact smaller in all directions, being confined in a narrower space.

The oval, central area also shows a certain amount of differentiation. Its upper limit is not at present clearly defined and the development of this part may be left out of consideration for a time. The junction of the axis of the haustorium with the mother root forms, in fact, a transitional region at present undifferentiated. In the lower part, however, a dense vertical shadow is seen in the middle line, extending almost to the surface of contact with the host's bark. The cells of this shadowed area appear to be dividing more rapidly in the vertical than in the horizontal direction and thus already appear to be elongated transversely to the axis of the haustorium. This elongation is shown well in figure 2d′ of Plate III, taken from a young haustorium of this age. The vertical shadow may be regarded as showing the first stage in the development of the gland.

The zone of the radiating cells described in the previous section (Plate III, fig. 1) has thus undergone considerable changes. But the cells of the haustorium, although somewhat disturbed, are still arranged in the same rows more or less at right angles to the host's surface and curving inwards to the axial line. It is still possible to trace continuous rows of cells from

the cortex right to the centre of the nuclear area, and it is difficult to draw any sharp distinction between cortical and nuclear regions where they pass into one another. The radial arrangement of the cells becomes gradually obscured in the nucleus by the rapid divisions taking place, while the cortex, as a whole, retains a radial arrangement for almost its entire existence (see paragraph 16).

8. It has been found difficult in the sections available to trace the stage just considered further, so much so that one is tempted to suggest two independent lines of development in *Olax* haustoria. The stage next met with shows sharp constriction at the top of the oval area and its consequent division into an upper and lower part. Two cases have, it is true, been met with where such a constriction may be thought to be actually taking place by the filling of a small triangular mass of cells on each side with starch grains, and thus simulating an ingrowth of the cortex, but the sections are not always very convincing. We shall assume that fig. 1 on Plate IV is the next stage in development, and that the small triangular areas *t t* divide the meristematic area into two parts.

The separation of nucleus proper from the vascular loop is well seen on Plates IV—VI. Leaving the vascular loop, which is usually quite immature, alone for the present, we find a series of remarkable changes taking place in the nucleus and cortex. The nucleus as a whole remains meristematic and unaltered save for the massing of plastic materials in its cells, but the gland develops rapidly, and largely at its expense. This organ has become sharply marked out as an oval region inside the nucleus, at first surrounded on all sides by protoplasmic cells (figs. 1—3), but, later on, growing to such a size and taking up so much for the nuclear space that it is not possible to say whether any of the latter tissue remains outside it excepting at the proximal end (fig. 4).

A great change has also taken place in the arrangement of the starchy and clear cells of the cortex. While the gland is

young and "unopened" there may still be some difficulty in locating the exact line of separation between the outer, starch-laden and the inner, clear tissues; the transition is as yet gradual. When, however, the gland is fully formed and throwing out its secretions, this line of separation is so striking that it arrests the attention at once (Plate IV, fig. 4, and Plates V and VI). This will be dealt with later.

The haustorium, as yet without penetration into the host's tissues, but possessed of the complicated structure shown in fig. 1 on Plate V, may be assumed to have reached its complete youthful form. As we shall see, the mere act of entering causes a complete change and presents us with an entirely different structure whose parts are difficult to recognize. The development having reached a certain stage, it will be well to consider the appearances in detail, as well as to compare the arrangement of the tissues with that of the haustorium of *Santalum* at a similar stage. For this latter purpose, we may refer to figure 22 on Plate V of Part I of the description of *Santalum* haustoria. A single glance at that figure is enough to show what great differences there are in the development of the haustoria in these two plants.

The nucleus in *Olax* cannot be made to agree with that in *Santalum*. In *Olax* there is a sharp separation between nucleus and vascular loop: in *Santalum* they are merged in one another and the nucleus passes some way up, projecting as a mass of parenchymatous cells in the median line between the two arms of the loop (Plate IX, figs. 2 and 4). The starch-filled cells in *Santalum* surround the nucleus closely and, further out, a distinct line separates them from the clearer outer cells. The reverse is the case in *Olax*, the denser cells being outermost. Moreover, this line of separation between the clearer and denser cell elements abuts, in *Santalum*, on the axial region at the middle of the vascular loop, in *Olax* opposite the middle of the gland, which is much lower down. The sucker in *Santalum* is formed of nucleus and cortex, but in *Olax* only the former takes part in its construction. And these differences are but the prelude to

others in the structure of the gland itself, of the collapsed layers and the vascular system. These parts of the haustorium will be dealt with in succession.

9. The gland is a very constant feature in the haustorium of *Olax scandens*, so constant that I have not been able to convince myself that it is ever absent excepting in the very smallest. This is at variance with what was observed in *Santalum*, where the gland was frequently absent and was regarded rather as an additional means of penetration in difficult cases.

It first makes its appearance as a dark shadow in the lower half of the nuclear axis (Plate III, fig. 2), and an examination of this shadow has shown us that it is caused by an accumulation of plastic materials in the cells, together with a very rapid sub-division into small cells transversely elongated (Plate III, 2d and 2d′).

At an early stage of the development of the gland a dark "cap" is seen to be formed over its upper, broader end, while the lower half is narrower and only imperfectly developed (Plate IV, figs. 1 and 2). The upper half rapidly expands, a wide clear "lumen" being formed traversed by faint dark horizontal lines, the cap at the same time becoming more pronounced and clothing the whole of the upper half of the gland. The lower half is narrower, is not bounded by such a dark layer but develops a lumen like that above it. Below the gland a dark vertical shadow is traceable connecting it with the host's root (Plate IV, fig. 2).

It will be well to examine such a stage carefully, because the glandular cells quickly undergo disorganization and, in the next stage (fig. 3), have already lost much of their character. The cap is seen to consist of a great number of very small cells closely packed together and densely filled with dark contents, being sharply marked off from the cells of the nucleus outside. These form the "bed" of the gland, giving rise to the secreting cells (Plate IV, 2b x). The walls of the lower half of the gland consist of similar cells, but they are neither so small nor so closely

packed, and pass by easy transitions into the rest of the nucleus (fig. 2a). The clear space, both above and below, is seen to be traversed by irregularly jointed, dark parallel lines, and as these can without difficulty be traced into the rows of cells at the sides composing the wall of the gland, it is fair to assume that they consist of the contents of broken down glandular cells. These are shown in Plate IV, figs. 2a and 2b, which illustrate the lowe and upper halves of the gland lumen respectively.

The next change which takes place in the gland is the great development of its lower half. This rapidly increases in breadth and becomes lobed. At the same time its walls become less distinct and the separation of the upper and lower halves becomes more pronounced (Plate IV, fig. 3). This stage does not, however, last long. While the upper half retains its cap, the lower increases in width until little if any of the nucleus is left at the sides. At the same time the gland tissues in this region become completely disorganised, and a large lumen is formed filled with a glairy substance and occasional indications of what were once rows of secreting cells (see Plate V, fig. e, where such cell remains are drawn). Meantime the shadow spoken of in describing figure 2 has become much more definite and, when carefully examined, proves to be a well-defined channel through the dense, compressed cells of the lowest part of the nucleus to the tissues beyond, whether of haustorium or host. This is the duct of the gland and is constantly present (see also Plate V, fig. d).

We see then that, while in *Santalum* the gland is formed by the separation of two sets of cells by a subcuticular secretion formed layer by layer until the lumen is filled (*Santalum*, Part I, Plate V), in *Olax* long lines of cells are decomposed, the contents becoming more and more attenuated until they disappear entirely in a glairy matrix. The gland in *Santalum* is more or less schizogenous, while that of *Olax* is essentially lysigenous.

10. In the stages thus far examined we have again and again had occasion to draw attention to the peculiar way in which the starchy and clear areas of the cortex are arranged. In the

earliest case examined (Plate III, fig. 1) a peripheral layer of irregularly arranged cells surrounds the actively growing part of the haustorium, and in this layer the cells are clear of starch. In the radiating cells of the growing part, on the other hand, starch is abundant, but it is denser in the outer cells, those nearer the host's root being clearer. This general arrangement has been met with in all subsequent stages of development, the densest layer being, however, formed further in in successive stages. It is fair to assume that the outermost clear cells have yielded up such starch as they had because they have ceased to take part in the life of the haustorium and (from the accumulation of calcium oxalate crystals) become moribund, merely functioning as a protective layer to the tissues within. Growth in the haustorium being centrifugal, it is natural to suppose that the comparative clearness of the inner layers is partly due to the cells being in a more meristematic condition. They are actively dividing and have protoplasmic contents. The deposition of masses of starch will presumably indicate that the meristematic condition has been passed or is in abeyance. The absence of dense masses of starch in the inner zone is thus readily explained, as also is the constant inward movement of the region where the masses of starch are densest, the outer cells becoming in turn permanent or moribund and yielding their starch to those within them as the latter lose their early meristematic condition. This region of greatest density is seen in thick sections as a dark shadow and may be followed by comparing the figures on Plates III—VI.

But while the comparative clearness of the inner layers presents no great difficulty in our study, when the gland appears we are confronted by a very puzzling phenomenon. The line of demarcation between dense and clear regions, at first very indefinite and difficult to locate, becomes sharp and the transition sudden, when the gland becomes mature. A perfectly clear inner zone with watery contents is differentiated, and this zone is bounded outwards by cells containing the densest masses of starch, the line of demarcation being thus intensified to the last degree. We have, if possible, to account for this curious fact,

completely at variance with all that we have seen in the *Santalum* haustorium

The line of separation appears to be closely connected with the gland, and always abuts on the nucleus nearly opposite to the middle of the gland, about where the "cap" reaches its lower limit. From the nucleus outwards it passes downwards on each side in a well-marked curve, more or less across the lines of growth, and terminates either indistinctly in the end of the cortical fold or curves round and ends sharply on its inner surface (Plate V, figs. 1 and b).

Obviously some other factor than the more or less meristematic condition of the tissues enters the case. In fact, the cells of the clear region soon *lose* their meristematic character and, when they reach the clearest stage, are permanent and more or less moribund. We may consider the food requirements of the developing tissues of the axis. Such would undoubtedly help to keep the inner cells of the cortex clear of starch and, with the great and sudden development of the gland, these requirements are intensified. The upper parts of the nucleus may be presumed to be supplied with nutriment by the strands of vessels from the mother root. But the needs of this rapidly developing upper part and the density of the tissues in this region cuts off, so to speak, the lower parts from this source of supply. The inner cells of the cortex are therefore laid under contribution. We have seen that at a certain stage the lower part of the gland swells enormously and rapidly becomes disorganized with the secretion of a mass of glairy substance. It is just at this stage that the inner cells of the cortex become cleared of their visible contents, and the cells thus cleared are exactly opposite to the swelling region of the gland. It appears probable therefore that the clearing of the inner cells of the cortex is due to the passage of their contents to the developing lower part of the gland.

And if this be the case, and explains the upward termination of the line of separation, it is not impossible that its downward continuation may be due to the same cause, less material being required as the scene of activity is receded from. This is not

offered as a full explanation of the phenomenon, and it is almost certain that other factors enter into the case. Such sharp lines of separation do not usually occur in homogeneous tissues rising from the same meristem, however much their contents may be wanted by the adjoining tissues (see for instance the action of the scutellum in emptying the endosperm of seeds), and there is evidently a profound alteration in the character of the cells in the clear zone at this time. Their after history shows that they are of no further use to the haustorium and take no further part in its activity. The remarkable clearness of the cells, taken together with their evident turgidity, lastly, suggests the possibility that the clear zone may act as a sort of transfusion tissue. It has already been noted that the lower part of the gland is widely removed from the vascular strands coming from the mother root (Plate VI, fig. 1). The formation of such masses of secretion as are seen in the final stage of the gland will require a considerable amount of water. Such a supply cannot presumably be rapidly passed from above—because of the absence of vascular continuity, the great development at the same time taking place in the upper part of the nucleus and the density of the glandular "cap." It is possible then that the clear zone represents a water reservoir on which the lower swelling part of the gland may draw when it reaches its period of maximum activity.

It should, however, be remarked that sharp lines of separation between starch-laden and clear cells are occasionally found in other parts of the haustorium of *Olax scandens*, although with less precision. In an older stage, for instance, as shown on Plate VIII, where the entry of the sucker into the host's root may be presumed to draw rapidly upon the surrounding tissues, the inner cells of the cortex become emptied of their contents and the line of separation between the clear and starch-laden cells is very distinct (Plate VIII, figs. 1 and 2 at x).

11. For entrance into the host's root the haustorium of *Olax scandens* appears, excepting in very small haustoria, to be

largely dependent on the dissolving action of the glandular secretion. In *Santalum* we saw that penetration could be effected without this organ and that, if the first attempt proved unsuccessful, the axial tissues next to the host were able to, so to speak, reconstruct the nucleus again and again, each time also producing a new pair of clasping folds. A compound haustorium was thus produced (*Santalum*, Part I, Plate V). There is only one nucleus and one pair of folds in *Olax*. Its haustorium is never compound. The reason for this is not far to seek. In the first place, the gland is exceedingly large and takes up the whole of the lower part of the nuclear meristematic tissues; and the tissues of the cortex immediately adjoining are, as we have seen, cleared of all their contents and, when the gland is mature, rapidly become moribund. In the second place, it is probable that the gland is a much more permanent structure than that in *Santalum*, and the "cap" in the upper part continues to supply cells which pour out their secretion long after the lower part is completely disorganized. One reason for assuming this long continued activity of the gland is the frequency with which the mature gland is met with in the sections. While such stages as are shown on Plate IV, figs. 1—3, are rarely met with, mature glands such as that on Plate V are quite common—indicating, I think, that the gland continues in this active stage for a considerable period, while it passes through the preliminary stages quickly. The need for secondary nuclei and cortical folds is not, therefore, felt by the haustorium in *Olax* and, if it were, there is no meristematic tissue left near the host's root which could produce them.

The figure on Plate VI appears to represent a very late stage of the gland: the whole of the lower part has been crushed, and the cap is still composed of many layers of secreting cells. There is some probability that the haustorium would have succeeded in entering this root, for a minute crack has appeared in the host's bark in the middle line and certain of the cells of the haustorium are projecting into it.

There are, however, other points of interest to be noted in the haustorium shown on this and the preceding plates. In

Plate V a fully mature gland is figured. Its lower part and the whole of the nucleus around it are completely disorganized, but some considerable growth has commenced in the nucleus above the gland, pushing the cap down into the lumen of the gland. The cells of this meristem are seen to be dividing so as to form rows of cells radiating from the lumen and they are also separated into two distinct regions, a median and a lateral (fig. c). The median strand consists of much smaller cells, divisions here taking place both in the radial and the tangential direction. This strand appears to be the first differentiation of what will be the axial plate of vessels. In Plate VI this nuclear meristem has grown considerably and the stage there illustrated may be taken to represent the last in a haustorium as yet wholly outside the host's root.

The downward thrust of the glandular mass exerts considerable pressure in the interior of the haustorium. This is seen in the flattened shape of the peripheral cells of the nucleus and those of the adjoining cortex. It is also seen in the crushing out of recognition of the lower part of the gland. But of more interest is its effect upon the zone of clear cells and the adjoining starch-filled parenchyma of the cortex. We have here in fact the first step in the formation of the *collapsed layers* clearly depicted. These are at first formed entirely from the outer cells of the clear layers (Plate VI, fig. 3) but, later, the outer starch-filled cells also take part, those about to be added to the collapsed layers losing their contents with fragmentation of the starch grains and becoming clear (Plate VI, fig. 2, and Plate VIII, figs. 1—3). A reference to what happens in *Santalum* will show that this formation of the collapsed layers is entirely at variance with what happens there. But this is not all. The collapsed layers of the mature haustorium in *Olax* are made up of three distinct parts, each formed at a different time and in a different manner, whereas in *Santalum* the collapsed layer on each side is uniform in its origin. The part of the collapsed layers formed at this stage of development in *Olax* is the lowest one. The middle portion is not formed until after penetration,

and the small, upper portion only after secondary thickening has greatly added to the diameter of the haustorium. The collapsed layers in *Santalum*, on the other hand, appear as lines of pressure in the cortex when the nucleus begins to expand, little or no difference being observable in the cell contents on either side of them during their formation (*Santalum*, Part I, Plate V, figs. 22 and 31, and Part II, Plate I).

As regards the vascular loop, there is thus far comparatively little change. In both this and the last stage, however, a horizontal plate of tracheides, divided in the middle line, has appeared immediately above the nuclear meristem (Plate V, fig. 1, and Plate VI, fig. 1).

12. No single instance has been observed among the 130 haustoria examined in the preparation of this paper of one in the act of entering the root of the host. We are justified in supposing from this that, as in *Santalum*, the haustorium enters very quickly. The tissue behind the gland, consisting of an immense number of small active cells charged with protoplasm, has become greatly elongated as soon as a breach has been made in the host's root. Profound changes in these tissues, chiefly due to the extension of the cells, have taken place in the act of entering, and it is, in most cases, difficult to trace their relative positions before and after penetration. The only method that has suggested itself of determining the extent of these changes is to select a haustorium which has entered some soft root or part of root and has thus been less distorted under the entering pressure, also which, by certain signs, as for instance the traces of a former gland, is seen to be in a youthful condition, and to compare it with that figured on Plate VI. This method has served to throw a good deal of light on the subject, as will be seen from figure 1 on Plate VII, where a young haustorium has penetrated a root of *Asparagus racemosus* but has as yet been unable to rupture the vascular cylinder, has not been cut off from the host's cortex by bands of cork and has a distinct trace of a former gland, all signs of comparatively recent entry.

This specimen is unusual in certain respects (due partly to the fact that the root entered is that of a monocotyledon) and therefore not altogether useful in the series, but it has the great advantage over the other sections obtained of forming a stepping stone between the younger gland-bearing stage and those which have penetrated and lost all signs of that organ, and, after a comparison with the stage shown on Plate VI, we are able to locate most of the tissues. The nuclear meristem has, indeed, changed almost out of all recognition, having thrust itself into the breach in the form of the sucker and swollen out there, besides developing a thick central strand of vessels. But, with the exception of the latter, the change in the tissues is chiefly such as would inevitably result from a great and sudden elongation of all the cells. There are probably not many more cells in the nuclear region of Plate VII than in that of Plate VI. The cortical cells have taken small part in the great expansion which has led to the formation of the sucker, excepting perhaps on the two sides where a small portion may have been dragged in. This might be expected from the much more meristematic nature of the nuclear cells than those of the surrounding cortex, and the small cortical masses dragged in have no part in the activity of the sucker. We see in this a further difference between *Olax* and *Santalum*. In *Olax* the sucker is formed of the cells of the nucleus, while in *Santalum* the cortex takes a distinct share in its formation, accompanying the nuclear tissues on each side. This difference has its explanation in the destructive action of the gland in *Olax* on all the tissues below it and at its sides.

The great advantage of the section on Plate VII, however, over all others met with of a similar age is that, by a careful comparison with that on Plate VI, we can at once lay our finger on the *zone of clear cells* with the collapsed layers outside them. We see also that the collapsed layers are being extended upwards, but this region is irregular in the section and will be referred to in a later specimen.

The median vascular strand passes upwards into a horizontal band of vessels (already indicated in the two previous Plates),

the base of the vascular loop, and the latter extends upwards, widely open, through the transitional region towards the mother root.

The region of the cortex with denser starch contents has in the section become narrower, the outer and inner cells of the radiating rows having become clear and devoid of contents.

13. The points referred to in the latter part of the preceding paragraph are more clearly brought out in the young haustorium figured on Plate VIII, entering a root of *Albizzia Lebbek*. Although the haustorium is still very young, the gland has completely disappeared, nor is the zone of clear cells certainly traceable without the aid of the section last described. In other respects this section is more regular than the last and shows the ordinary course of the haustorial development better. The root invaded is that of a dicotyledon and shows the sucker lobes passing on each side along the cambial line and throwing back the two cortical wings of the host's root. The vascular strand is simple, no secondary thickening having taken place. The tissues derived from the nucleus are sharply marked off from those of the cortex, being separated by collapsed layers or being readily distinguishable from the nature of their own contents (figs. 1 and 2).

The lower part of the collapsed layer curves abruptly inwards round the ends of the cortical wings of the host. This inward projection is of constant occurrence and is difficult to explain. As we shall see later on in this paragraph, it is probably derived from nuclear tissue and corresponds with the small bay of clear cells marked *d* in figure 2 of Plate VI. Whatever its origin, it undergoes no further development, but the part of the collapsed layer below it still increases in thickness, receiving accessions of crushed cells both from the zone of clear cells within and from the cortical cells outside it (fig. 3). Such cortical cells as are about to be added to the collapsed layer can be readily traced by their almost total lack of contents. The first change that appears in them is the breaking up of the starch grains into very fine particles and these, later on, disappear entirely. The cell walls

remain white while those of the unaltered starch-filled parenchyma outside become slightly discoloured and browned (figs. 1—3).

The formation of the middle part of the collapsed layer is well seen in the section. It is formed entirely from cortical cells and follows the line of junction of cortex and nucleus. Its mode of origin from the innermost cortical cells is seen to agree with that described above for the increase in thickness of the lower part (fig. 3), so much so that the middle and lower portions of the collapsed layer appear as an undivided whole and form an unbroken curve, the inward projection half way up alone indicating the place of junction (figs. 1 and 2). The upper limit of the middle part of the collapsed layer is indicated by the ending of the clear cells outside it (fig. 2 *x*). The starchy cells beyond retain their character during the life of the haustorium, losing their contents very gradually. The third or uppermost part of the collapsed layer is unimportant, appears only in old haustoria with secondary thickening and follows a different course (see paragraph 16).

The axial tissues at this stage require a word of explanation. When the nuclear meristem undergoes its great extension and thrusts itself downwards into the host's root, its cells are stretched to their utmost limit. In one place this extension is too much for the cohesion of the tissue and it is ruptured, forming a characteristic and well-marked lacuna (fig. 2, *lac*, but better in Plate VII, fig. 1). The cells above and below this lacuna, being subjected to very different degrees of tension, are not affected in the same way. While those above become greatly elongated (Plate VIII, fig. 2, *a*), they remain connected with one another and retain their radial arrangement (they correspond with the cells marked *a* in Plate VI, fig. 2). They have delicate protoplasmic sacs and are readily distinguishable from the starchy cells which were early pushed in between the nucleus and the vascular loop (Plate IV, fig. 1, *t*).

The cells below the lacuna are more difficult to explain, and it is not altogether certain to what part of the nucleus they belong. They form a sort of "nest" of cells, oval in shape, rounded towards the collapsed layer and drawn out downwards

in the direction of the sucker, and show a well developed and constant collapsed layer in the middle (Plate VIII, fig. 2, *b*). This nest of cells is apparently little affected by the changes which have taken place. They appear to lie in a sort of eddy in the conflicting currents of growth around them. As far as can be seen, they correspond with the area marked *b* in fig. 2 of Plate VI, and have been dragged inwards and downwards so as to occupy a horizontal instead of vertical position. If this is the case, the cleared cells at *d* in the same figure would naturally, as suggested above, be crushed and persist only as a minor collapsed layer, as at *b* in fig. 2 of Plate VIII.

The starchy cells of the cortex are well seen. The radially arranged cells are, as in Plate VII, cleared of contents both outwards and inwards and have a band of densely packed cells in the middle. And, in passing, it is remarkable how sharp is the line of demarcation between the starch-filled and the clearer cells about to be added to the collapsed layers (see end of para. 10). The denser layer does not undergo much further change, its cells have apparently entered the permanent stage and their walls are brown and firm. Such masses of cells, frequently with remnants of starch in them, are met with right on till the end of the life of the haustorium.

14. We have now studied the structure of young haustoria which have succeeded in penetrating monocotyledon and dicotyledon roots, and it is hoped have succeeded in bridging over the gap in the series before and after penetration. We have seen that the zone of clear cells, ending upwards opposite the middle of the gland, is traceable into the tissue that is thrust back against the collapsed layers by the opening cortical wings of the host's root. The lower part of the collapsed layers, at first arising from crushed cells of the clear zone, is afterwards added to by cells of the starchy cells outside, which have lost their contents. The middle part arises where nucleus joins cortex, above the former glandular region, and is formed entirely from the outside, that is from cortical cells. These lower and middle

portions coalesce and form the ordinary collapsed layers of the mature haustorium, an inward process permanently marking the point of junction. In such a mature haustorium the upper end of this collapsed layer points to the top of the nucleus or to the angle formed by the vascular strand of the axis and the base of the vascular loop. This development of the collapsed layers in *Olax* is very different from that described for the haustorium of *Santalum*. In *Santalum* the collapsed layers are formed much further out and their upper end passes well outside the whole vascular loop, and, in non-median sections, right round it. These differences are illustrated by the diagrams 2—5 on Plate IX; figs. 2 and 3 represent young and mature stages of the haustorium of *Olax*, 4 and 5 of *Santalum*. The collapsed layers are indicated by the letters *c. l.*

The gland, which is such a marked feature in the young haustorium and is apparently constantly present in haustoria of any size, leaves no trace behind it in the ordinary mature haustorium, thus again contrasting greatly with the behaviour in *Santalum*. This constant absence of traces of the gland in older sections at first caused great surprise. It was surmised that its disappearance was due to the disorganized nature of the gland in its older condition, to the great force with which penetration is effected and the hardness of the woody cylinder of the host's root against which it is pressed. Sections cut later through soft roots confirmed this view. In 12 cases distinct traces of a former gland have been met with, and these are all or almost all in attacks on soft-tissued hosts, *Azima tetracantha* and *Asparagus racemosus* being typical examples. Every section cut of haustoria penetrating these roots shows traces of the gland (Plate VII, figs. 1 and 2). The part of the gland left is presumably the last remaining cells of the cap of densely crowded cells at the top of the active gland and possibly portions of the duct. The comparison of *Olax* and *Santalum* in this respect will be rendered clear by a reference to the diagrams 3 and 5 on Plate IX, where *gl* indicates the remains of the gland after penetration.

The sucker cells in contact with the host's root are similar to those in *Santalum*. Those at the ends of the lobes are secreting, pouring out the characteristic (yellow) mucilaginous substance in which the cells are seen to radiate (Plate X, fig. 2). After the secreting edge of the lobe has passed and connection has been established between the cells of haustorium and host, the organ becomes absorptive, and reticulated vessels are formed along the main lines of transport. The cells in contact with the host's root are elongated and form a palisade-like layer which is specially distinct in old haustoria which have lost their contents (Plate X, fig. 1). In all these respects the resemblance between the suckers of *Olax* and *Santalum* is very close.

15. It will have already been noted that the vascular tract in the lower part of the haustorium in *Olax* differs from that in *Santalum* in the absence of a pith or median parenchymatous tissue. There is a single, median plate of vessels in place of two parallel ones. The absence of this parenchyma is perhaps one of the chief peculiarities in *Olax*, as it is present in all the other haustoria of the series examined, and it is accompanied by great differences in the early stages of development of the haustorium.

In *Santalum* the nucleus is seen to project upwards between the two diverging arms of the vascular loop (Plate IX, fig. 4, dotted line) and, in older stages, its upper limit is marked by a transverse collapsed layer (fig. 5). The vascular loop is open below and, in young stages, its two arms pass downwards into procambial strands on either side of the nucleus. In *Olax*, on the other hand, the vascular loop is closed below by a transverse plate of vessels and the nucleus is separately formed below this region (fig. 2). The procambial strand is formed above the gland in the median line and the vessels are not developed until the gland has been pushed down against the woody cylinder of the host's root (fig. 3).

Figure 1 on Plate VIII shows a very young stage of the vascular tract in *Olax* haustorium, the vascular loop passing down

into a single vertical plate with a delicate layer of cambium on each side. In figure 1 on Plate VII a median section is shown through an older haustorium. Secondary thickening has commenced in the vertical strand, and it is interesting to note that this usually commences some way below the vascular loop, in fact, at a point about opposite to the lacunæ inside the middle parts of the collapsed layers. These two and subsequent thickenings are illustrated by a series of diagrams 6—10 on Plate IX, each one of which is taken from an individual haustorium which has been chosen as the type of a class. Figures 6 and 7 show the early stages already described ; figure 8 corresponds with the haustorium shown in figure 1 on this Plate. The thickest part of the strand gradually passes upwards in succeeding stages until it embraces the base of the vascular loop (figs. 9 and 10). At this the final stage, the whole vascular mass assumes a wavy outline due, to all appearance, to its being penetrated by broad medullary rays.

The elements of this vascular mass are mainly narrow tracheide-like vessels with simple circular perforations at their ends, and of remarkably uniform character (Plate X, fig. 3). The following differences have been noted in various parts of the axis. In the region of greatest thickening, at the base of the vascular loop, the elements are short and arranged in rows derived from the same cambial mother-cell, with medullary rays here and there between them. There is little difference in the inner and outer vessels unless it be a slightly greater width in the outer ones. Passing down the axis, the medullary rays are less conspicuous, the vessels become longer and, if anything, narrower, until they separate near the host's root to isolated strands of elongated elements. The vessels in the region of the loop show greater differences. Those in the lower half are very long and narrow, but remain uniform among themselves. Above the middle, as might be expected, this regularity is disturbed and broader elements make their first appearance. The vessels increase in diameter upwards until, in the mother root, ones are found with many rows of pits. The number of pits met with across the walls of the various vessels forms a convenient mode of comparing

their width. Those of the protoxylem, those in the end of the sucker and those in the lower half of the vascular loop usually have 1—3 rows of pits. The somewhat wider, outer vessels formed by the cambium of the axis show 3—4 rows, while the vessels of the transitional region (above the middle of the vascular loop) and the mother root may have as many as 6 to 10.

The sections thus far dealt with in the present paper have all been transverse, that is, cut across the root attacked. Sections in this direction, as we have seen in *Santalum*, include more of the tissues of both host and haustorium than those cut in any other plane. To understand the vascular system of the axis, however, horizontal sections will be necessary (*i.e.*, cutting the haustorium across its axis and the root attacked, if in the section, tangentially). Such sections are shown on Plate XII (figs. 1 and 1a), and the arrangement of the parts can be readily made out. Note in these figures *px*, the protoxylem, with scattered parenchymatous elements, *x* the secondary xylem with its numerous medullary rays *mr*, and the cambium *c*. The uniformity and small size of the vessels is clearly shown in transverse and horizontal sections, and on a comparison with a section of the mother root, it is seen that the haustorial vessels correspond best with those found in young roots. The larger vessels found in older roots are not met with in the axis of *Olax* haustoria attacking other plants. Those on *Olax* itself will be referred to in paragraph 18.

The section drawn on Plate IX (fig. 1) being cut in the plane of the medullary rays, the latter are not seen. The vascular strand bifurcates above and passes with its various elements upwards round the vascular loop into the transitional region. In *Santalum* attention was drawn to the fact that, in the upper part of the vascular loop, the vessels became indistinct, hyaline and filled with gum, and this region, occurring in all older haustoria, was called the "interrupted zone." There is no trace of this feature in the vascular loop of *Olax scandens*, although it is markedly present in sections of *Thesium*, *Osyris*, *Opilia* and especially *Cansjera*.

An examination of the diagrams on Plate IX will show that in the haustoria examined there is no great development of secondary thickening (see for instance the case of *Santalum* in *Santalum*, Part II, Plate IX) and, from the frequent clearness of the tissues in the older stages, it is probable that the life of these organs is comparatively short. A certain number of references to the age of haustoria are scattered through the literature on root-parasites. Thus Granel[1] remarks that the haustoria even of perennials do not usually last longer than one year. Leclerc du Sablon[2] noted that older plants of *Pedicularis* form new suckers each year. Heinricher[3] showed that the haustoria of *Lathræa* can live for more than a year and asserts that Krause has proved the same for *Bartschia alpina*. Kusano, in his studies of the haustoria of *Buckleya Quadriala* in Japan, speaks of the growth of the haustorium keeping pace with that of the root to which it is attached, and of haustorium and root growing thus together for as many as a dozen years with cambiums in contact. In the tropics we have no means of determining the age of haustoria by means of annual rings as did Kusano, for these are not developed with any distinctness. But we have, on the other hand, some reason to believe that the activity of the haustoria is short-lived, because of the regular decay of the vascular system at a certain point, the interrupted zone. On the whole one is led to believe, from the haustoria so far examined, that the functional activity of haustoria in the *Santalaceæ* and *Olacaceæ* in the tropics is not long continued, may indeed cease long before the actual growth of the haustorium does.

In older haustoria of *Santalum*, where much secondary thickening has taken place, it was noted that the inner layers of secondary wood in the axis became discoloured and filled with gum, the protoxylem, curiously enough, not suffering this change

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1 Granel, Note sur l'Origin des suçoirs de quelques Phanerogames Parasites. Bull. d. l. Soc. Bot. de Fr. XXXIV, 2. IX. 313—321. 1887.

2 Leclerc du Sablon, *ib.*

3 E. Heinricher, Die grünen Halb-schmarotzer. III. *Bartschia* und *Tozzia*. Jahrb. f. wiss. Bot. XXXVI. 665—752. 1901.

but remaining white and clear. A much more pronounced duramen is to be seen in the haustoria of *Buckleya* described by Kusano attached to various Coniferous roots, the duramen of the haustorium keeping pace in growth with that of the host, as does the cambium. In *Olax* the protoxylem at an early stage becomes discoloured in like manner and a few cases have been noted in which the inner layers of the secondary wood are also thus discoloured. This discolouration is partly due to brown substance filling the lumina of the parenchyma between the vessels (Plate IX, fig. 1 and diagrams 6—10).

16. An old stage of *Olax* haustorium is shown in fig. 1 of Plate X, the host being *Casuarina equisetifolia*. The sucker lobes, working along the cambial line, have almost completely surrounded the vascular cylinder of the attacked root. Nevertheless its abundant development of new secondary bundles, both in the centre and in the cortical wings, suggests that the *Casuarina* root has as a whole suffered comparatively little injury. The haustorium, on the other hand, as is usual in such old stages, has cells emptied of all contents, the layer of cells in contact with the vascular cylinder is pronounced and the remaining tissue remarkably clear. This clearness of tissues has been regarded as a sign of waning activity of the whole organ in *Santalum* and it has been assumed that such haustoria are moribund, a point of view adopted by Solms-Laubach[1] in his study of *Thesium*. The section now being studied is of further interest in that it shows the connection between haustorium and mother root and the development of the upper part of the collapsed layers.

The collapsed layers have in this case reached their utmost development and extend upwards for a short distance on either side of the vascular loop. The lower and middle portions have already been described in detail in paragraph 13; the upper portion is, like them, developed entirely from cells of the cortex.

1 H. Graf zu Solms-Laubach. Ueber den Bau u. Entwickelung der Ernährungsorgane Parasitischer Phanerogamen. Jahrb. f. wiss. Bot. Vl. 1867-68.

A small inward projection sometimes, as in this case, marks the junction of upper and middle portions, and it is easy by this means to distinguish the three parts of the collapsed layer. There is no marked differentiation here of the cells which are about to become crushed and added to the layer, but this is not the case always, as is seen from a study of Plate IX, fig. 1, where the clearing of the cells for the formation of the uppermost part of the collapsed layers is well shown (*u. c. l.*). This portion of the collapsed layers may be regarded as directly due to the increase in thickness of the axis of the haustorium by secondary thickening. As the thickest part moves upwards, it is followed by an upward extension of the collapsed layers on each side. We see then that the collapsed layers in *Olax* consists of three parts formed at different times and in different ways, all, however, arising entirely from the collapse of cortical cells which have lost their contents.

The zone of radiating cells outside the collapsed layers, so closely connected in former stages with the deposition of large starch grains, has entered on its last phase. The radial arrangement is still visible, but the starch has all gone and, in its place, masses of calcium oxalate crystals have been deposited. Thus, throughout the life of the haustorium the curves of growth have been retained in this part of the cortex, an additional proof that it takes little or no part in the penetration of the host's root. Such was not the case in *Santalum ;* but in certain cases, notably in attacks on *Pithecolobium Saman* and *P. dulce*, a narrow band of similarly arranged cells was found on the outer sides of the collapsed layers, having all the appearance of cells derived from a secondary meristem (*Santalum*, Part II, para. 7). From a consideration of the sections of *Olax scandens* haustoria examined it appears possible that this group of cells in *Santalum* is rather a remnant of the former curves of growth than a new formation.

We saw in our study of the earliest stage of *Olax* haustoria met with (Plate III) that the rows of cells forming the body of the haustorium were separated from the older, irregularly arranged cells outside them by a lacunar band of crushed cells.

This separating layer is constantly present and may be regarded as an *outer collapsed layer*. It is clearly seen in the figure under discussion (Plate X, fig. 1). Such outer collapsed layers are not infrequently found in *Santalum* (cf. *Santalum*, Part II, para. 7) and those in *Olax* are, as in that case, probably due to the shrinkage of the outer cells of the cortex. We shall refer to these outer collapsed layers in dealing with the connection between haustorium and mother root.

The deposition of crystals of calcium oxalate has been referred to on several occasions and has been regarded as evidence of a complete cessation of activity in the tissues bearing them. At first present only in the outer layers of cells under the corky surface, later on they appear in masses in the radiating cells. They are also frequently met with in the parenchymatous cells inside the vascular loop and in the little nest of cells opposite the ends of the cortical wings of the host, tissues clearly of no further use to the haustorium. Their occurrence in the clear zone is rare. Within the collapsed layers, that is, in the original nuclear area, they are also rarely found. In the few cases observed, they form, in this region, long strings of minute black crystals passing through a series of cells in a long line.

The mother root from which the haustorium was developed is seen cut across on the right hand of the top of the section (Plate X, fig. 1). The space traversed by the vascular bundles uniting it to the haustorium has been termed the transitional region. The strands of vessels in the axis of the haustorium are continuous with similar elements right up into the mother root. They are thus accompanied by the cambium. But the vascular strand of the axis is devoid of bast. The phlöem elements of the mother root are continued some way down, but cease in the transitional region. By observing their lower limit we shall have another means of judging the position of the line of separation between the haustorium proper and the region above it. The bast in *Olax* roots is distinguished as a layer of thin-walled cells densely filled with contents which are coloured light brown in spirit material. In this brown, undefined layer isolated groups of sclerotic cells

of peculiar appearance occur, always accompanied by long rows of square cells with single crystals. We may term these "fibro-crystal" groups and their form is seen in Plate X, figures 4 a—f. These fibro-crystal masses are frequently found in the transitional region of the haustorium but do not (with the exception to be mentioned below) appear lower down than the middle of the vascular loop.

Although there is no distinct endodermis visible in the *Olax* roots examined, many sections show in the upper parts of the transitional region isolated brown cells of great distinctness, their position being in general outside the bast. It is not possible to connect these cells with the endodermis, and all that can be said is that they occur in the endodermal region. They are traceable from the mother root into the transitional region and, as might be expected, the outer collapsed layer is seen frequently to be in direct continuation with them. They are not found lower down than the middle of the vascular loop.

Cork is a constant feature outside the haustorium, being much more commonly found than in sandal haustoria. It usually ceases at the ends of the cortical folds, but, in not a few cases, has been traced inside the latter as far as the upper ends of the cortical wings of the host's root. In one or two cases it has been met with further in, aborted sucker lobes are seen sometimes to be surrounded by it and, in one case, the whole sucker has been cut off by its own cork formed in thick layers.

17. The relation between haustorium and host need not be dealt with so fully as it has been in *Santalum*. To do so would entail much repetition. An attempt is rather made to compare the haustoria of *Olax* with those of *Santalum* in their action on the root attacked.

Penetration follows closely the lines indicated in *Santalum*. The sucker is tongue-like at the commencement, excepting where very dense bands of sclerenchymatous cells bar its way. This form is retained in certain roots where the tissues are soft and watery, as in *Boerhaavia repens*, where a broad tongue passes

right into the woody cylinder without any division into lobes. In monocotyledons like *Asparagus* the sucker proceeds thus as far as the sheath of the woody cylinder and undergoes no further differentiation, actual entry into the woody cylinder not having been observed (Plate VII, fig. 1). In *Azima tetracantha* the rule is that the sucker, after passing through the soft cortex, passes down one or more of the broad medullary rays in tongue-like branches. Such cases are rare and are obviously determined by the structure of root attacked. In ordinary dicotyledons with a fairly solid central cylinder the sucker, on reaching it, divides into two broad lobes, one on each side, which follow the cambial line, destroying it as they proceed.

The following variations may be noted. In a few species the sucker lobes, before reaching the woody cylinder, have strayed tangentially in the cortex. Such cases appear to be common in *Acacia arabica*, *Casuarina equisetifolia*, *Streblus asper*, and have been noted in one or two other species. In most of these, however, the sucker has ultimately reached the cambium by one or both lobes or by a new development of the tissue in the middle of the sucker. Where a sucker lobe has thus wandered in the cortex, the cells become after a while clear and moribund, like those of haustoria in contact with the woody cylinder. A very distinct palisade-like tissue is thus sometimes developed and this is especially well seen in sections of haustoria attacking *Casuarina equisetifolia* (Plate VII, fig. 3). One-sided entry, largely connected with this wandering in the cortex, is rare, indicating great regularity in the penetration of ordinary dicotyledonous roots, and the form figured (Plates VIII, IX and X) is by far the commonest and hardly deviated from. In the same way the woody cylinder is rarely entered. *Azima tetracantha* is an exception and is apparently always pierced along the broad medullary rays till the woody cylinder is divided up into sections. This species, with the soft *Boerhaavia repens* are practically the only cases noted.

The wings of the cortex of the host are occasionally attacked and destroyed. These wings are then in most cases cut

off by the formation of cork below the injured places. Corky layers surrounding the wings appear with great frequency, thus protecting them from further injury. Cork is also found as with *Santalum* in a number of cases in the tissues opposite to the ends of the sucker lobes.

Secondary thickening in the root attacked is far more general than in the attacks of *Santalum*, and the cortical wings in a great number of cases join in this secondary wood formation. Such wood, formed after the attack has reached the cambium, deviates at first from the normal, having thinner elements, less sclerotic cells and fewer vessels in the wood (cf. *Santalum*, Part II, para. 19, *Note*). The formation of gum or thyloses in the cavities of the vessels opposite the cells of the sucker occurs as under the attacks of *Santalum* haustoria, and in many cases this formation is markedly confined to the region between the ends of the lobes of the sucker.

On the whole, the haustoria of *Olax scandens* rarely fail to enter a root attacked, possibly thanks to the complicated and long-lived gland. Moribund haustoria have been much more rarely met with than in *Santalum*, but the tracts of country from which the collections were made were very different and no definite conclusion can be drawn from this. The test for full activity or waning power is the relative absence of contents in the cells. In *Olax* it is chiefly the older haustoria which are thus emptied, such as have developed secondary thickening. The entry, as we have seen, is regular and usually along the cambial line. But when this has been effected, the haustorium does not appear to be so destructive of the host's tissues as that of *Santalum*, whether in the wings or in the woody cylinder.

The action of the sucker cells upon the tissues of the host opposite to them seems to be similar to that noted in *Santalum*. In places, the influence can be seen at a distance by the formation of new bands of sclerenchyma or cork opposite the point of attack, the formation of gum or thyloses in the vessels or the yellowing of bands of sclerotic fibre in the cortex. But there is no clearing of starch in the host's root opposite the

haustorium as has been described by Fraisse in attacks by *Osyris alba.*[1]

The effect of the secretions on starch appears to be rather slow. In not a few cases starch grains have been found in the layer of secretion and disorganized cells of the host after all traces of the cell-walls have disappeared (Plate VIII, figs. 4 and 5). This seems to suggest that the ferment secreted by the sucker cell is chiefly cyto-hydrolytic and, when we consider the abundant assimilating foliage of the parasite and its need before all things of water and salts, this does not appear strange. A somewhat similar state of affairs was observed in *Santalum* (Part II, para. 33) where Peirce's[2] observations on *Cuscuta* were alluded to. Brown and Morris[3] report that in the germination of barley the tarch is not acted on until a certain amount of solution has been effected and the cells have been isolated. Newcombe[4] has given an extreme case in the ferments of germinating seeds of *Lupinus* and *Phœnix*, the ferments dissolving the cell-walls being hardly at all diastatic. It is all the more interesting to note Fraisse's observation quoted above that, opposite to the sucker cells of the haustorium of *Osyris*, a zone of cells free of starch indicates the region of its activity.

18. It was noted in *Santalum* that self-attached haustoria, that is, such as were fixed on other sandal roots, differed in certain respects from those attacking foreign roots. The relations between host and parasite in these cases varied. In several instances it was difficult to separate the tissues of the two where

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[1] Fraisse Sur le Parasitisme de l' *Osyris alba*. Comptes Rendus Acad. Sc. Paris, 30 Jan. 1905. Fraisse states that every root attacked, whether perforated or not, shows a region devoid of starch, "qui délimite le zone d'action du mamelon haustorial."

[2] G. J. Peirce, on the Structure of the Haustoria of Some Phanerogamic Parasites. Annals of Botany, VII, 1893. Peirce describes the action of the sucker cells of *Cuscuta glomerata* upon the mesophyll of balsam leaves. He states that the large thin-walled papillate cells dissolve and bore the walls of the cells they are in contact with, making perforations little wider than their own diameter. They dissolve the contents rather slowly, starchy substances first, protoplasmic later.

[3] J. R. Green, On Vegetable Ferments. Annals of Botany, VII, 1893.

[4] F. C. Newcombe, Cellulose Enzymes. Annals of Botany, XIII, 1899.

they touched one another. In others considerable resistance was offered by the root attacked. The sucker was carefully cut off in the usual manner and fresh growths took place in the cortical wings, by which the sucker as a whole was squeezed, the host acting as if engaged in occluding a wound (*Santalum*, Part II, Plate XVI).

In self-attached haustoria in *Olax* fusion of the tissues is the rule (Plate XI, figs. 1, 2 and 6). This is not however all, for the difference between such and ordinary haustoria is much greater than in *Santalum*. All the vascular tissues of the mother root are continued down the entire length of the haustorium and, at the end, are in connection with the similar tissues of the host's root.

We saw in paragraph 15 that the vessels of the axial strand of the *Olax* haustorium are uniform and narrow. In self-attached haustoria wider elements make their appearance, giving the whole strand an entirely different appearance (Plate XI, figs. 1, 3 and 6 ; Plate XII, figs. 2, 2a and 2a[1].) These wider vessels are identical in structure with the broader vessels of the secondary wood in *Olax* roots. Bast also is formed throughout the haustorium (Plate XI, fig. 1, and Plate XII, fig. 2). Not only are the fibro-crystal bodies found all along the outer edge of the cambium in the axis, but well marked sieve-tubes with callus-plates are readily distinguishable, and staining with water-blue shows that they are present in very large numbers (Plate XI, figs. 3 and 4). From an inspection of this Plate, where these facts are illustrated, it is evident that a thorough fusion of host and parasite has taken place and that the cambium passes from one to the other so as to place the wood and bast in organic connection (fig 6), the formation of wood and bast in the haustorium keeping pace with that formed in the woody cylinder of the host (fig. 1). This has not been observed elsewhere in *Olax* or *Sandal* haustoria, but the description of *Buckleya* by Kusano indicates that in older haustoria the wood formation keeps pace with that of the host. Another point of interest is that, in self-attached haustoria, the vessels at the end of the sucker lobes before secondary thickening

has commenced, swell up considerably and become shorter and even globular (figs. 2 and 5).

The occurrence of sieve-tubes in the haustoria of green hemi-parasites has not been, it is believed, observed before. Peirce,[1] who investigated a number of cases, found that in *Lathræa*, *Brugmannsia* and *Cuscuta*, colourless parasites, sieve-tubes were abundant, while they were absent in *Viscum*, a green hemi-parasite, a result which is in agreement with what has been noted in *Santalum* and *Olax* and was also proved for *Buckleya* by Kusano. The presence of this complete vascular connection between host and parasite, usual only in cases of holo-parasitism, opens the way for interesting speculations and experiments regarding the nutrition of such plants. And a more careful examination of all the other cases of self-attached hemi-parasites is called for. It is not likely that *Olax* will be singular in this respect.

Botany School, Cambridge,

June 1907.

[1] G. J. Peirce, *ib.*

APPENDIX.

List of hosts on whose roots haustoria were examined in the preparation of the present paper :—

Acacia arabica.
Acacia leucophloea.
Albizzia Lebbek.
Asparagus racemosus.
Azima tetracantha.
Boerhaavia repens.
Cadaba indica.
Capparis sp.
Carissa spinarum.
Cassia siamea.
Casuarina equisetifolia.
Cephalandra indica.
Dichrostachys cinerea.
Feronia Elephantum.
Jasminum sessiliflorum.
Jatropha gossypifolia.
Melia Azidarachta.
Morinda tinctoria.
Ocimum sanctum.
Olax scandens.
Opuntia Dillenii.
Pentatropis microphylla.
Phaseolus ? sp.
Phyllanthus simplex.
Pithecolobium dulce.
Pongamia glabra.
Rivea hypocrateriformis.
Ruellia prostrata.
Solanum trilobatum.
Streblus asper.
Tragia involucrata.
Vitex Negundo.
Zizyphus Oenoplia.
Zizyphus Jujuba.

DESCRIPTION OF PLATES.

PLATE I.—

(All the figures excepting 4 are of natural size.)

Fig. 1. Ripe fruit of *Olax scandens*. Note the calyx fused with the pericarp to near the top.

Fig. 2. Germinating seed with primary root emerging and bending downwards. Note the catuncle-like outgrowth of the endosperm.

Fig. 3. A further stage in germination. The hypocotyl forms a delicate green loop above ground, the seed being just below the surface. The lower part of the stem and the upper part of the root are white and thickened. The root is covered with root-hairs. A section across such a root is shown in fig. 1 of Plate II.

Fig. 4. Section across the seed in such a stage as that shown in fig. 2. The cotyledons are folded in the centre of the oily endosperm, their exposed surfaces having a distinct epithelium-like layer of cells.

Fig. 5. A young seedling six weeks old. The upper part of the hypocotyl is green and above ground; the lower, subterranean part is white and swollen. The node with the scars of the cotyledons is seen at the top and a first pair of leaves has been unfolded. The whole root-system is richly covered with root-hairs.

Fig. 6. A seedling grown in pure sand for six months. The root-system is copiously branched, but the frequent swellings (due to eel-worms) show it to be in an unhealthy condition. Root-hairs are still abundantly present, but no haustoria are seen. The curious fasciated ending of the root is due to its growth round the base of the pot. A number of leaves are developed, but several have already fallen. The shoot is assuming a dorsi-ventral habit.

Fig. 7. A seedling one year old, also grown in pure sand. It is obviously unhealthy, most of the rootlets being dead and leaving behind them characteristic scars filled with brown mucilaginous matter. The main root is distorted by eel-worms and a few haustoria are present.

Fig. 8. A seedling of *Olax scandens*, found in nature, attached by numerous haustoria to an older plant of the same species. The specimen is interesting in that it was through its being dug up that the parasitism of *Olax* was first discovered. It is preserved in the Cambridge Botanical Museum.

PLATE II.—

Fig. 1. Transverse section through part of the root of a young seedling (see fig. 3 of Plate I), showing the development of root-hairs.

Fig. 2. Part of a small rootlet of *Olax* found in nature (natural size and magnified). Numerous haustoria are being formed, and it is to be noted that, while the rootlet is covered with root-hairs, the haustoria are smooth and free from them.

Fig. 3. Root-endings of *Olax scandens* found in nature (natural size and magnified).

Fig. 4. A rootlet from a pot-plant attached to a pebble by a small haustorium (natural size and magnified).

Figs. 5 to 8. Haustoria of *Olax scandens* (figs. 6 and 7 natural size and 5 and 8 magnified).

In 5 note the peculiar lobing of one haustorium: this is not uncommon. Also note the scars left by former haustoria. The root attacked is that of *Azima tetracantha* and the figures are twice natural size. In 6 a series of haustoria, apparently terminal, are applied to a root of *Albizzia Lebbek*. A comparison with a series of specimens shows that the haustoria in *Olax* as in *Santalum* are never really terminal (see fig. 8 where a small portion of the vascular cylinder is all that remains of the mother root beyond the haustorium). Fig. 7 shows two large haustoria also apparently terminal. In fig. 8 a typical haustorium is shown as well as its burrowing action into the bark of the host's root.

PLATE III.—

Fig. 1. A non-median section through a very young haustorium. The various tissues are illustrated by enlarged drawings at a, b, c and d.

Fig. 2. An older stage of development cut so as to show the entrance of the bundle of vessels from the mother root. The parts are arranged as in fig. 1, but considerable development has taken place.

Note especially the "shadow" of starchy cells, *b*, the oval light-coloured nucleus and the dark median shadow of the gland, *d*. 2d, a portion of such a stage of the gland further magnified. 2d^1, a similar section from another, slightly older gland. The cells of the gland are elongated horizontally.

PLATE IV.—

Four stages in the development of the gland. Fig. 1 shows a stage connected with those on Plate III. At *tt* the cells of a small triangular area on each side become charged with starch. The oval area of Plate III is thus separated into two parts, an upper, the vascular loop, and a lower, the nucleus proper.

After the stage shown in fig. 2, no definite structure can be seen in the lumen of the gland. Figs. 2a and 2b show portions of such a stage magnified further. At *x* is the bed of the secreting cells which form a cap round the upper part of the gland. In fig. 3 the lower part is lobed, while in fig. 4 the gland is mature and the cells of the upper part of the nucleus have commenced actively dividing so as to press the gland downwards. Note the duct *d*.

A change may be observed in these figures in the position of the densest, starch-filled tissue of the cortex, which is found further in in succeeding stages until it is met by the zone of clear cells. The line of demarcation between the outer and inner parts of the cortex becomes more and more distinct until, when the gland is mature, it is exceedingly sharp.

PLATE V.—

Transverse section through a haustorium attached to a root of *Melia Azidarachta*, with a mature gland. The stage is similar to that in fig. 4 of the last Plate. Detailed drawings are added of the various parts. Fig. a shows the junction of nuclear and cortical cells at the top on one side, the cortical cells being filled with starch and those of the nucleus with protoplasmic contents. In fig. b the line of separation between the starchy and clear cells of the cortex is shown. The median shadow of the upper part of the nucleus is drawn in fig. c together with a few tracheides forming the base of the vascular loop, and the upper part of the cap of the gland. Fig. d shows the duct and fig. e some of the more distinct cells at the edge of the lumen in the lower part of the gland.

PLATE VI.—

A unique specimen of a haustorium immediately before penetration. The vascular loop is well developed and a number of vessels are formed. The median shadow *c* in the upper part of the nucleus is the first stage of the vascular strand of the axis. By the growth of this part the cap is being thrust down into the lumen, the tissues there being completely disorganized. When the cap is pushed down, a part of the nucleus, *b*, is left behind on each side. This portion is separated from the region of the cap by a bay of clear cells, *d*.

The clear zone of the cortex, *cl.*, is devoid of all contents and its cells are moribund. The first traces of the collapsed layers *c. l.*, are observable at the junctions of the clear and starch-filled cells of the cortex. The root attacked is one of *Zizyphus Oenoplia* and a small crack is seen in the bark, just opposite to the opening of the duct of the gland.

In fig. 3 a small portion of the cortex is figured lower down, where clear and starchy cells adjoin one another and the collapsed layer is about to be formed, at first from the crushed cells of the clear zone and, later, from the inner cells of the starch-filled zone, the cells having meantime lost their contents.

PLATE VII.—

Fig. 1. A transverse section through an *Olax* haustorium penetrating a root of *Asparagus racemosus*. The sucker is tongue-like and has reached the woody cylinder of the host, *x*. Note *lac*, lacuna, *gl*, traces of a former gland.

Fig. 2. A part of the gland trace from another section through the same haustorium. *x*, woody cylinder of the host's root. A portion of the lumen remains and it is bounded by the mucilaginous secretion poured out by the cells. The indistinct lines show successive layers of this secretion.

Fig. 3. The end of the lobe of a haustorium which has wandered in the cortex of a root of *Casuarina equisetifolia* and has not succeeded in reaching the wood of the host. The sucker cells are moribund and, as in all such cases in *Casuarina*, form a very pronounced palisade tissue. They are embedded in brown substance largely produced from sucker cells when in a state of activity.

Fig. 4. The edge of a haustorium, the central part of which has succeeded in penetrating a root of *Vitex Negundo* as far as the cambium. It is presumed that the figure represents in some

sort the manner in which penetration takes place in the first instance. The cambium, *c*, with the layer of phlöem, *ph*, outside it, has been destroyed opposite the point of attack, but the host's root has developed a protective layer of cork, *ck*, at this point in place of the phlöem.

PLATE VIII.—

Figs. 1 to 3. Transverse section through a young haustorium which has penetrated a root of *Albizzia Lebbek*. The sucker is lobed and follows the line of the cambium in the host's root. Portions are magnified further in figures 2 and 3.

Note in fig. 2, *a*, the cells of the upper part of the nucleus which have become elongated in penetration, the adjoining cells of the cortex remaining unaltered: *lac*, the lacunar region not very well developed in this case: *b*, the nest of cells: *x*, the sharp line of separation between the starchy cells of the cortex and those which are about to be added to the collapsed layer.

Fig. 3. A portion of the lower part of the collapsed layer. It is being formed by the addition of crushed cells both from the clear zone within and the cortical cells without, *cl*, clear zone *c. l.*, collapsed layers, *co*, cortex.

Fig. 4. A portion of one of the wings of the bark of *Azima tetracantha*, showing the comparatively slow solution of the starch grains, *s*, sucker cells, *scl*, sclerotic cells of the bark, *st*, starch grains, the cell walls containing them having been dissolved away, *ck*, cork being formed on the inner face of the wing. *st* and *scl* are indistinct and imbedded in yellow secretion from the sucker cells.

Fig. 5. A portion of the woody cylinder of the same root of *Azima tetracantha* showing the persistence of the starch grains in a medullary ray. *s*, sucker cells, *v*, vessel, *m. r.*, medullary ray of the host. The starch grains are lying in the yellow secretion after the cells which contained them have been dissolved away.

PLATE IX.—

Fig. 1. Transverse section through a haustorium fixed on a root of *Capparis* sp., which has developed secondary thickening. Note a couple of fibro-crystal masses at the top of the loop. The lacunar region of the nucleus is well seen, as also the nest of cells below the lacuna. The lower and middle parts of the collapsed layers are well shown as also the cells becoming clear for the formation of the upper part *u. c. l.* Note the protective

cork formed in the host's root round the edge of each lobe of the sucker, and the continued formation of wood in the part of the cylinder thus protected.

Figs. 2 and 3. Diagrams of *Olax scandens* haustoria in the gland stage and after penetration. *c. l.*, collapsed layer. The dotted line signifies the outline of the nucleus *n. gl*, remains of a gland.

Figs. 4 and 5. A similar pair of diagrams for *Santalum album*.

Figs. 6 to 10. Diagrams of successive stages of secondary thickening in the haustorium. The darker, inner portion signifies older vessels breaking down and resembling duramen, although this layer is not usually pronounced.

PLATE X.—

Fig. 1. An old, moribund haustorium fixed on a root of *Casuarina equisetifolia*, for a description of which see the text (paragraph 16).

Fig. 2. The end of a sucker lobe in a haustorium fixed on a root of *Jasminum sessiliflorum*. The sucker cells are seen to spread out in a mass of dark brown substance which bathes the tissues of the host. The colouring matter is probably developed from the host, but the bulk of the matrix is secretion. Note the latest addition from the secreting cells as a clear border outside the ends of some of the cells.

Fig. 3. A small portion of the vascular strand of the axis of the haustorium with secondary thickening taking place. The vessels are uniform and bear from two to three rows of pits. The cambium passes outwards almost directly into the irregular parenchyma and there is no trace of bast formed from it.

Note the circular perforations of the vessels where they meet one another.

Fig. 4, a—f. A series of drawings of the fibro-crystal masses such as are seen cut across in various directions at the top of fig. 1. Fig. 4 a is taken from a transverse section of a young root of *Olax scandens*.

PLATE XI.—

Self-attached haustoria of *Olax scandens* (see the text, paragraph 18).

Fig. 1. Shows such an attachment under low power. The vascular strand of the axis is much developed and accompanied by bast (as indicated by the fibro-crystal masses and the medullary rays) right down to the end of the sucker. At the latter point the xylem, cambium and phlöem are seen to be in direct continuation of those of the host's root.

Fig. 2 shows the end of the sucker of another self-attached haustorium. It is difficult to state where the sucker ends and the host begins. The vessels are enlarged at their ends (see fig. 5).

Fig. 3. A portion of the vascular system of the axis in the section shown in fig. 1, further enlarged. It should be compared with fig. 3 of the last Plate which, however, has been inadvertently drawn on a larger scale.

In haustoria fixed on *Olax*, large and small vessels occur as well as fibro-crystal masses and well-developed sieve-tubes. These are absent in all other cases examined.

Fig. 4. Sieve-tubes from fig. 3 magnified further.

Fig. 5. The endings of the vessels in the sucker lobes before secondary thickening has commenced. They are almost globular in form (see fig. 2).

Fig. 6. A small portion of fig. 1 magnified to show the junction of the xylem of haustorium and host. *p*, vessels and parenchyma of haustorium, *h*, medullary ray and vessel of the host. *p* is cut longitudinally and *n* transversely.

PLATE XII.—

Horizontal sections through *Olax* haustoria (1) on *Albizzia Lebbek* and (2) on *Olax scandens* itself.

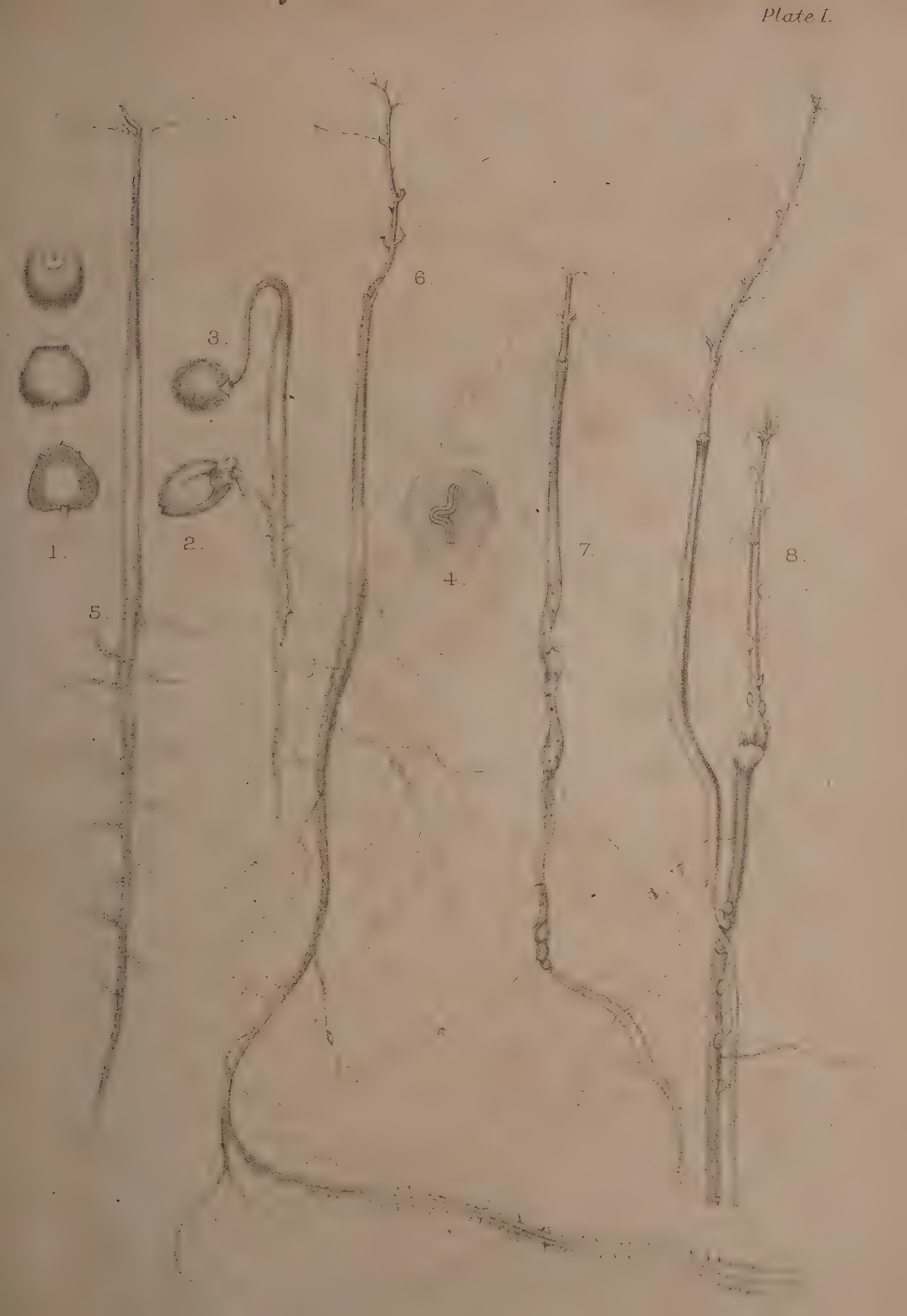
Fig. 1. *px*, protoxylem, *x*, xylem, *c*, cambium, *lac*, lacuna, *c. l.*, collapsed layer.

Fig. 1a. Portion of the last figure more highly magnified, *mr*, medullary ray. The section shown in fig. 1 is cut so that one side (the left) is higher up in the haustorium than the other. The right-hand portion shows a section through the axis opposite the lacuna. That on the left traverses the base of the vascular loop, shows the lattice-work of vessels in longitudinal section, and again cuts across the vessels transversely as they pass upwards. Traces of bast are discernible outside the cambium in this latter part.

Fig. 2. The haustorium cut is a good deal older than that in fig. 1.

A great development of bast with fibro-crystal masses, *cr*, is seen in the axis.

Figs. 2a, $2a^1$. Parts of the vascular system showing the great vessels, as compared with the small uniform ones shown in fig. 1a.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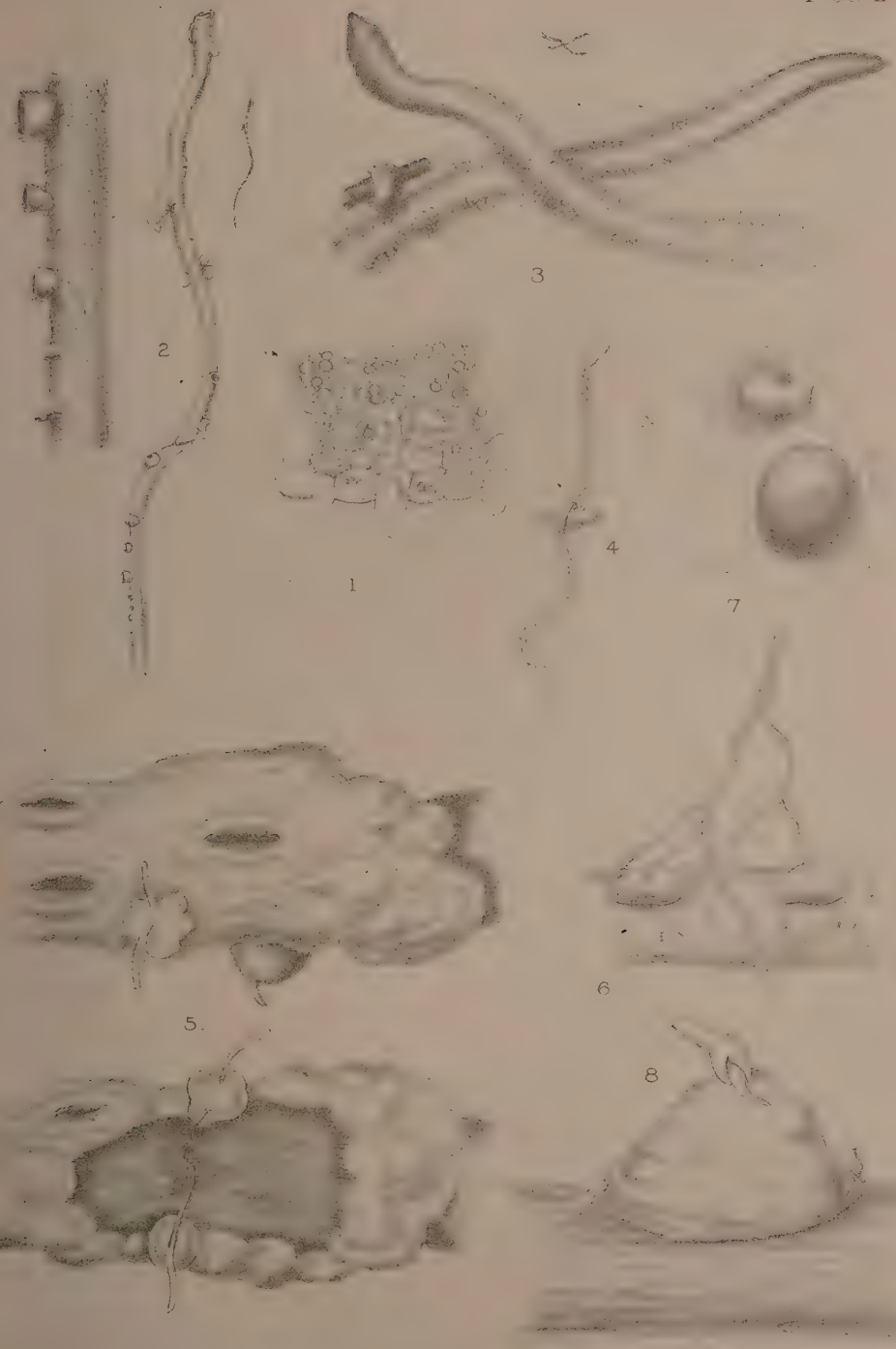

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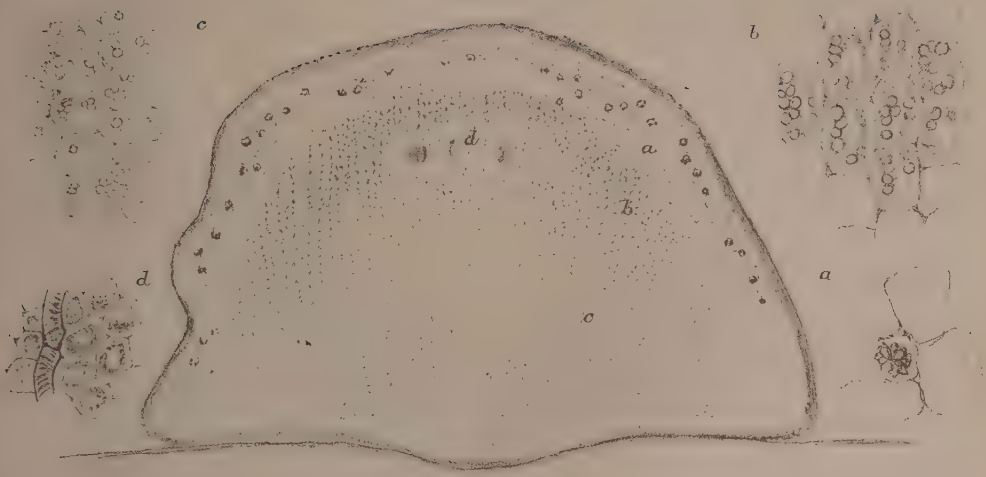

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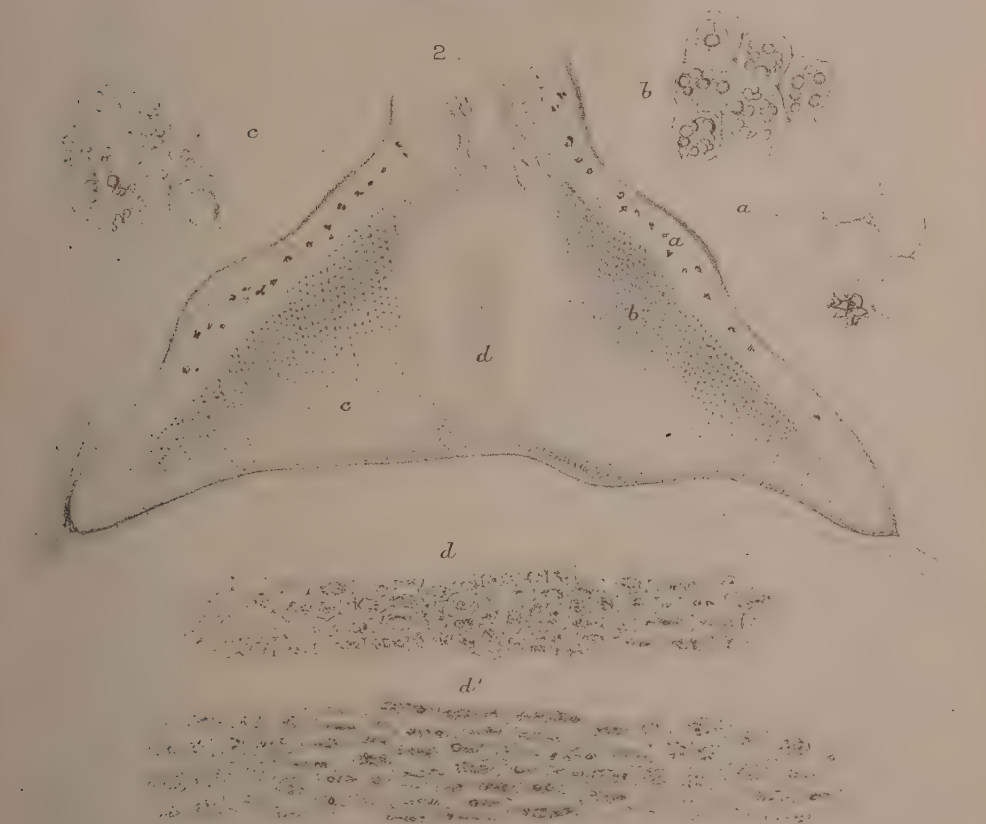

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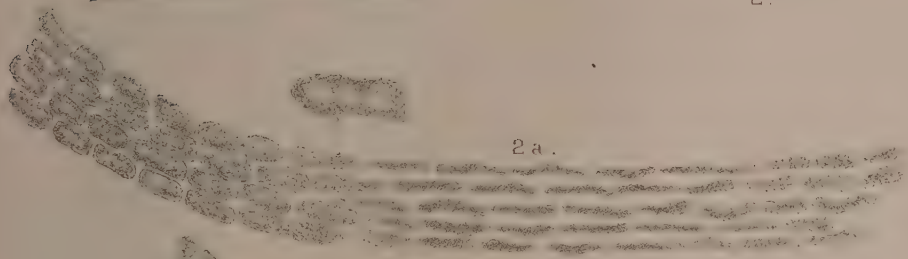

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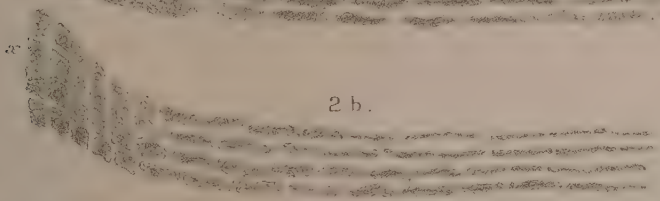

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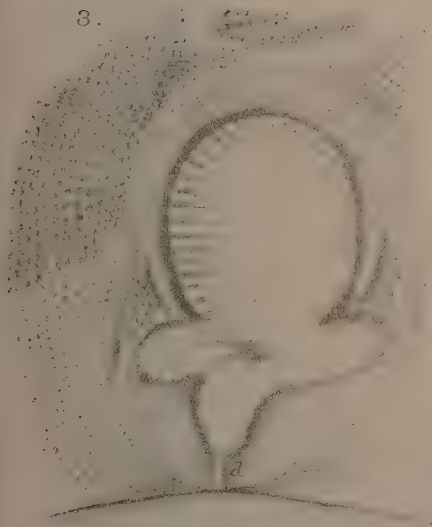

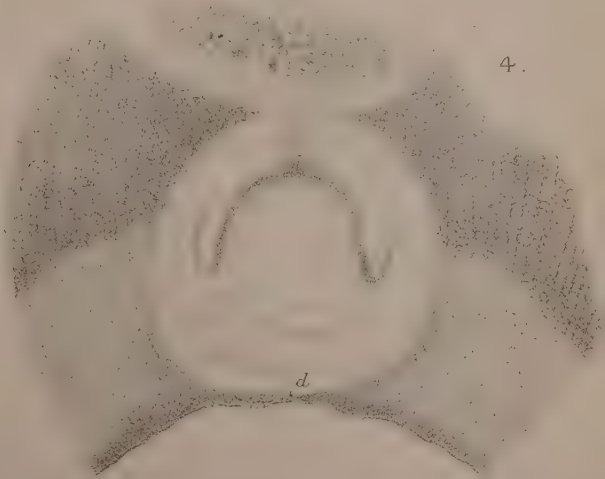

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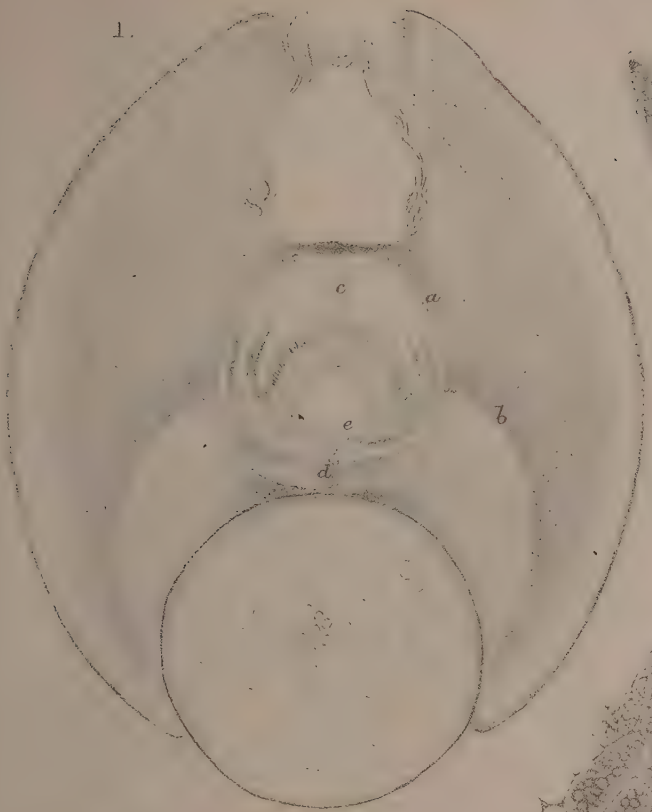

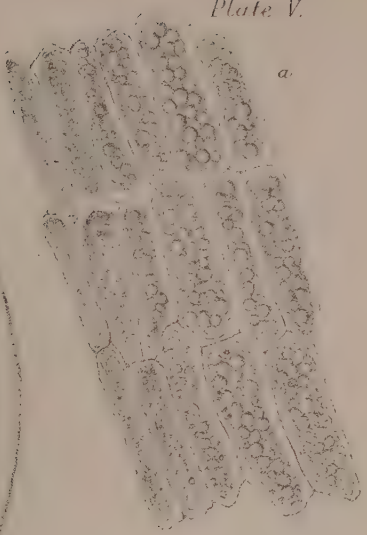

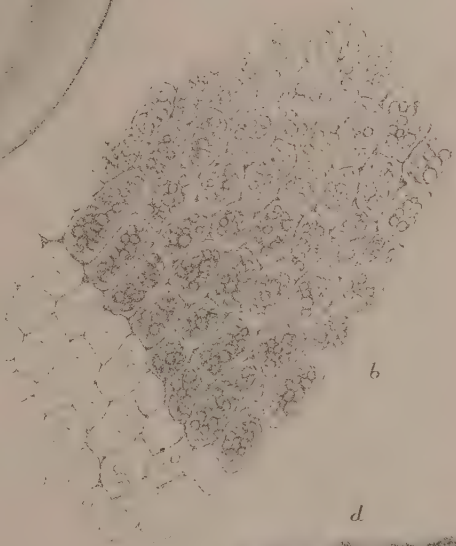

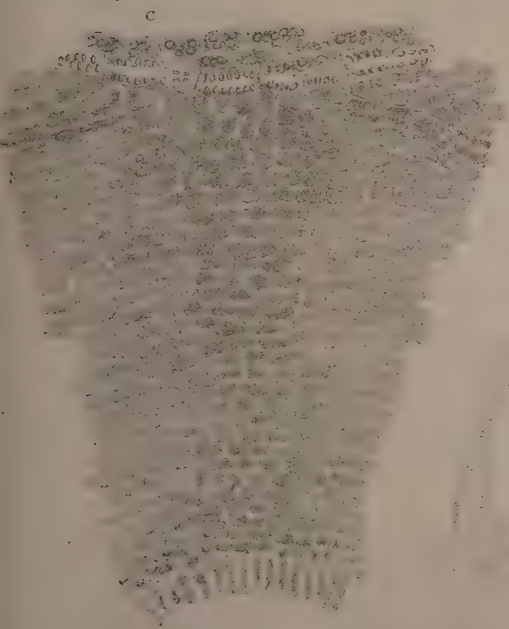

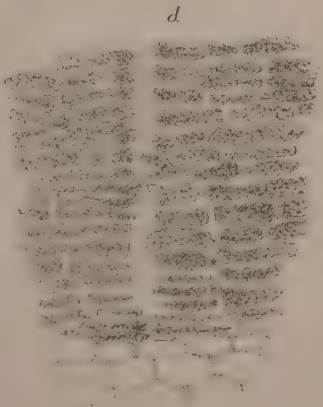

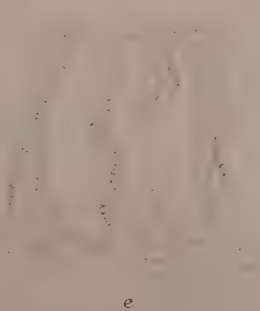

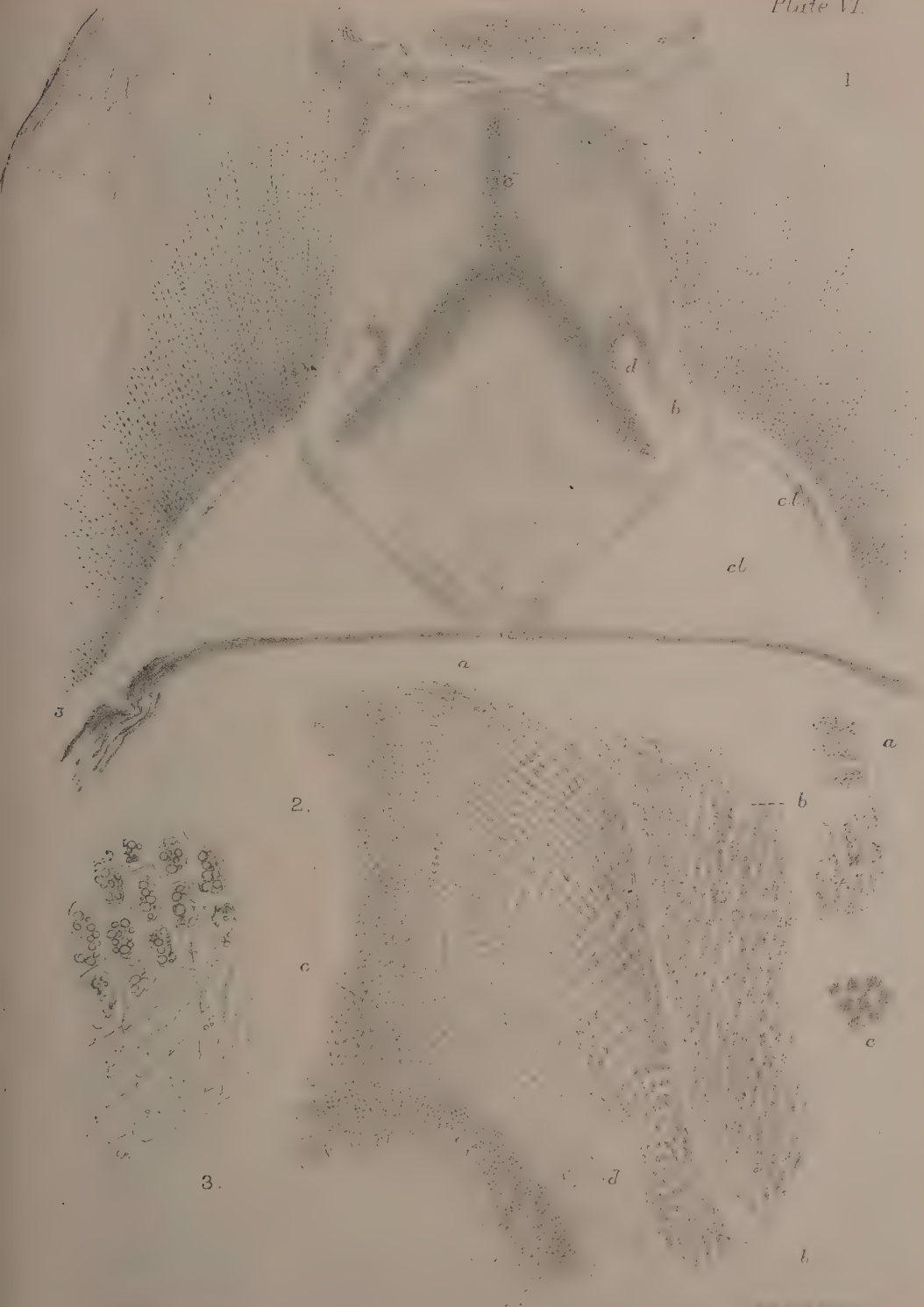
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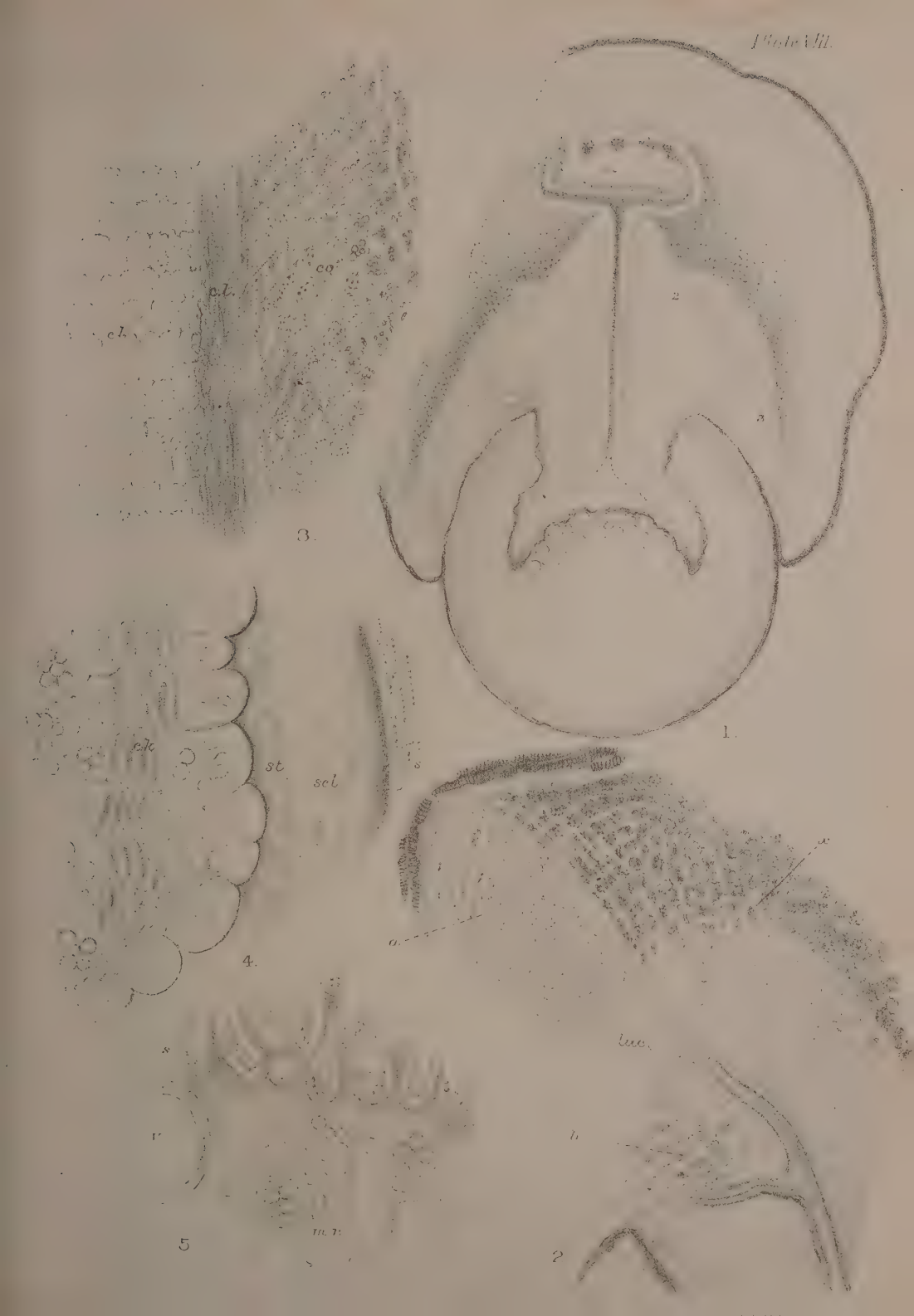
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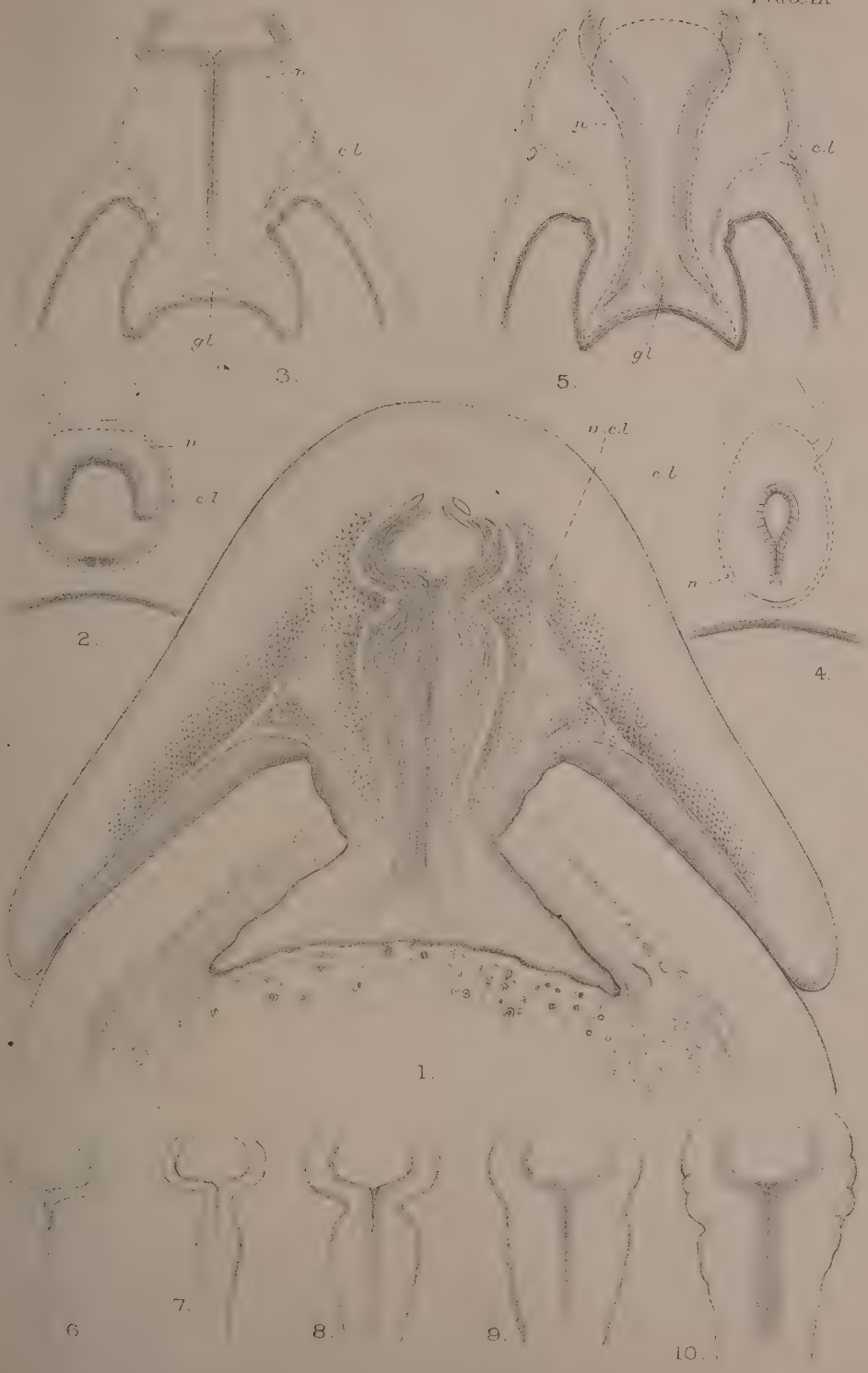

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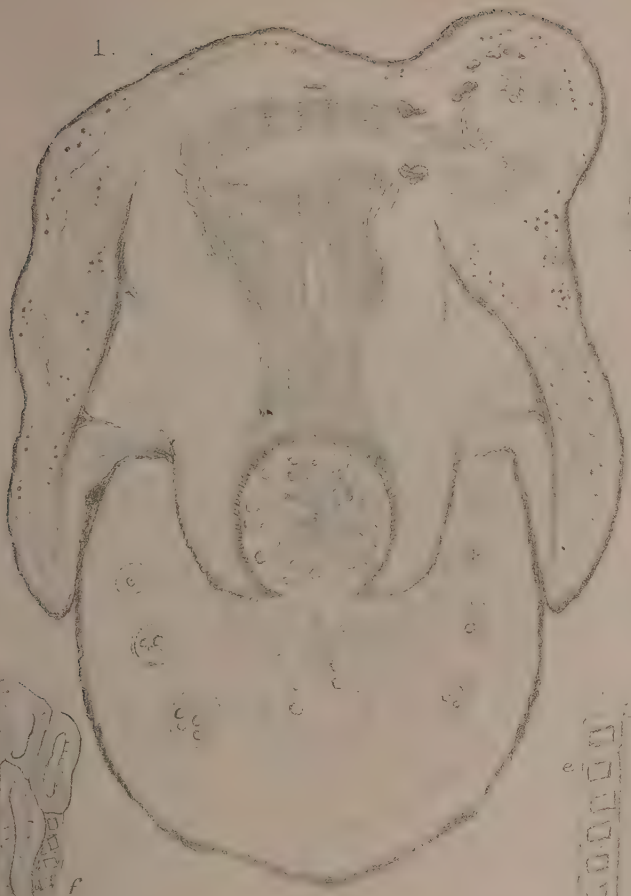

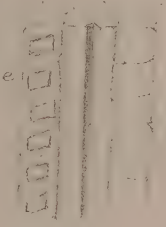

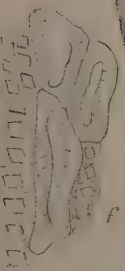

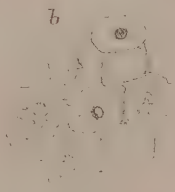

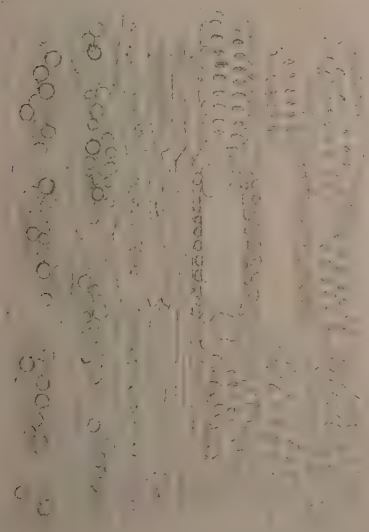

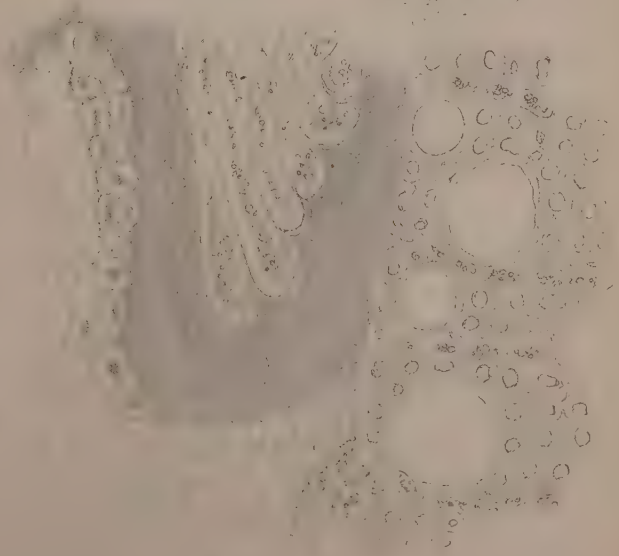

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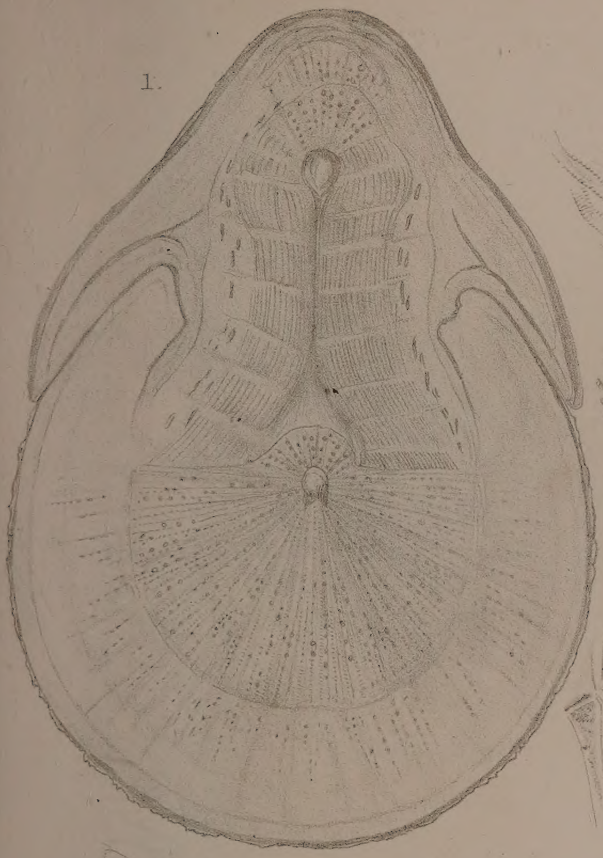

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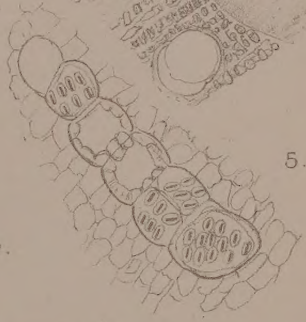

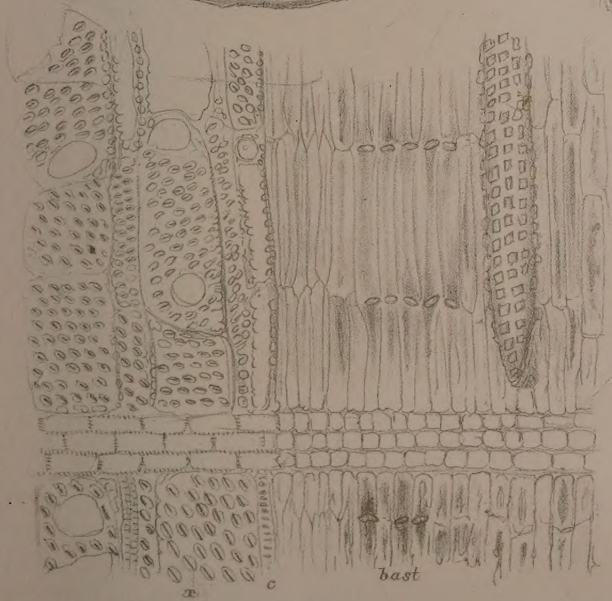

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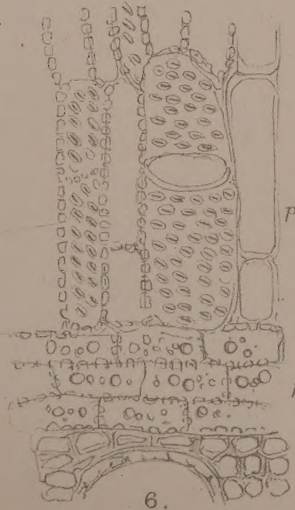

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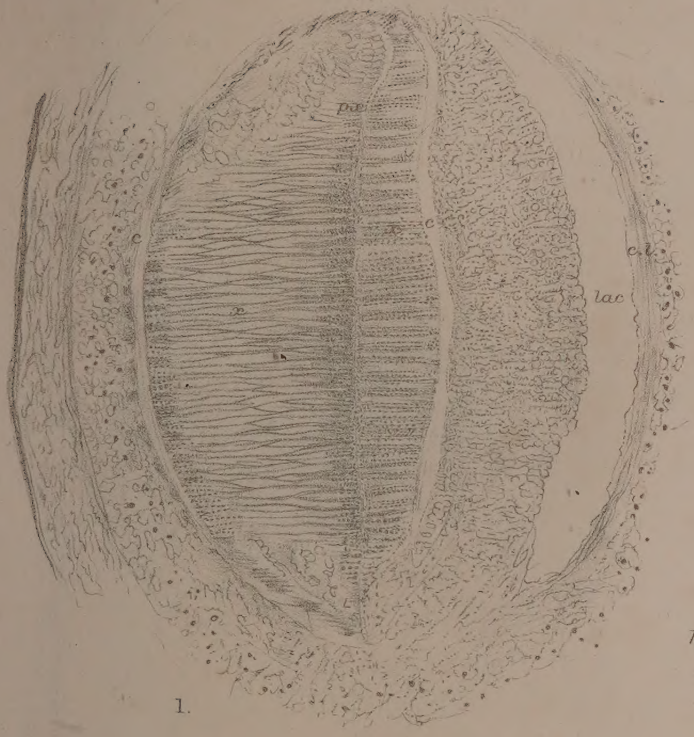
Plate XII.



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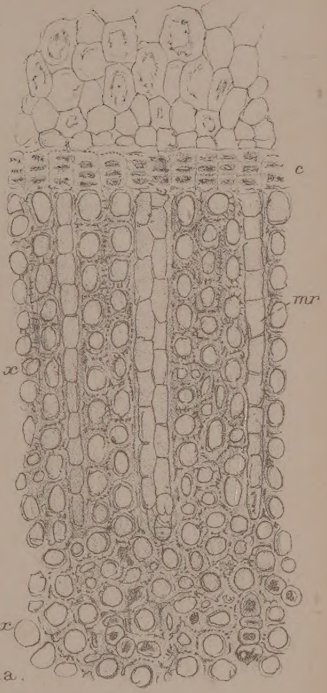

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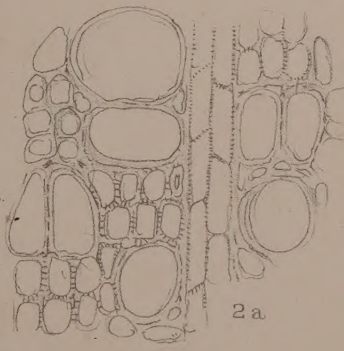

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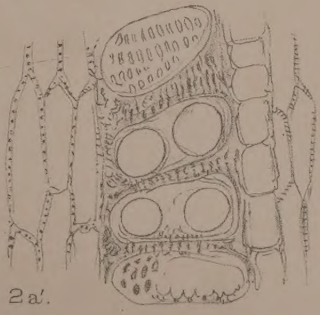

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